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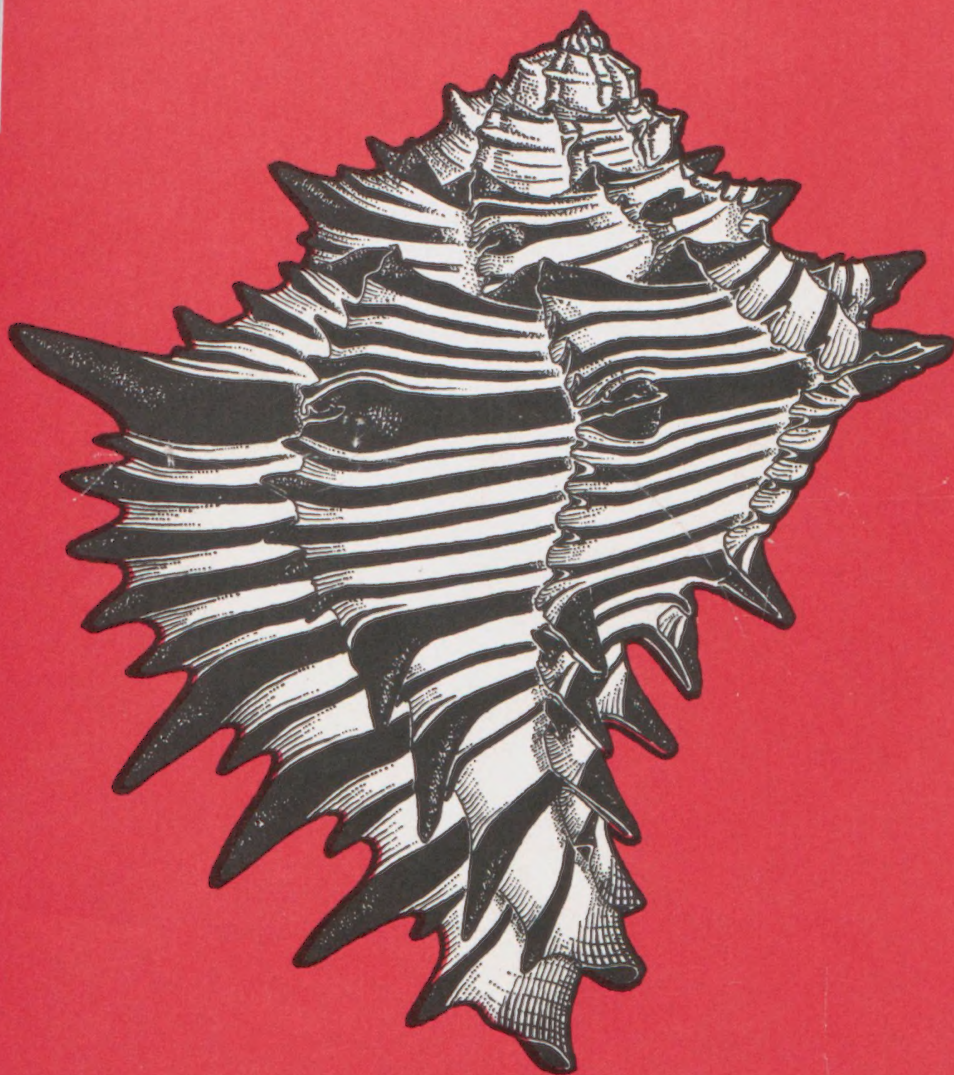
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PAPHIA (PROTAPES) (BIVALVIA: VENEROIDEA) IN THE ARABIAN SEA, WITH THE DESCRIPTION OF A NEW SPECIES

P. GRAHAM OLIVER¹ AND EMILY GLOVER²

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Abstract: The genus *Paphia* in the Arabian Sea contains taxa belonging to the subgenera *Protapes* and *Paratapes*. The species of *Protapes* and *Paratapes* are revised using shell morphometric analysis. Five taxa are recognised of which four are distinguished at the species level with the fifth given sub-species status only. A new species, *Paphia* (*Protapes*) *rhamphodes* is described from the coast of Oman and the Arabian Gulf. *Paphia* (*Protapes*) *gallus* is regarded as distinct from *P. (P.) sinuosa*, the former not extending north of the Malabar coast and absent from the Arabian Sea. A new subspecies *P. (P.) gallus bombayana* is recognised from NW India and hypothesised to be a result of clinal and ecological influences. The remaining taxon, *P. (P.) cor* is tentatively retained in the genus *Paphia*.

Key words: Taxonomy, Bivalvia, Tapetinae, Arabian Sea.

INTRODUCTION

Venerid clams are a predominant component of inter-tidal and sub-littoral sand and mud flats. They have been widely used as food and are a major part of prehistoric shell middens in the Gulf region. The most common inter-tidal species in the Arabian Sea are *Circenita callipyga* (Born, 1798), *Amiantis umbonella* (Lamarck, 1819), *Marcia flammea* (Gmelin, 1791) and a species of Tapetinae with affinity to *Paphia* subgenus *Protapes*. It is this latter species that formed the impetus for this research for not only did it appear to be undescribed it brought into question the number and identity of *Paphia* species in the Arabian Sea.

Early lists (Melvill & Abercrombie, 1893; Melvill & Standen, 1907; Melvill, 1928) suggest that five species with affinity to *Paphia* are present; *Venus textile* Gmelin, 1791; *Venus undulata* Born, 1780; *Venus malabarica* Chemnitz, 1782 = *V. gallus* Gmelin, 1791; *Venus cor* Sowerby, 1853 and *Venus sulcosa* Philippi, 1847. In the only revision of the Tapetinae, Fischer-Piette & Métivier (1971) indicate under the genus *Paphia* the following species from Arabian waters, *P. textile*, *P. undulata*, *P. malabarica* and *P. cor*. They believe that *P. sulcosa* is limited to eastern Australia and synonymise it with *P. crassisulca* (Lamarck, 1818). They do not state which species the Arabian records of *P. sulcosa* should be referred to but Oliver (1992) referred all Aden material present in the Shopland collection to *P. gallus*.

The conception of the subgenus *Protapes* being monotypic (type species = *V. gallus*) is widespread, only Matsakuma (1988) referring more than a single species to *Protapes*. This suggests that the original definitions of *Paphia* and *Protapes* do not encompass the degree of variation shown by the critical characters such as outline, sculpture and proportions of the pallial sinus. Consequently this study not only revises species level taxonomy but reviews the generic diagnoses.

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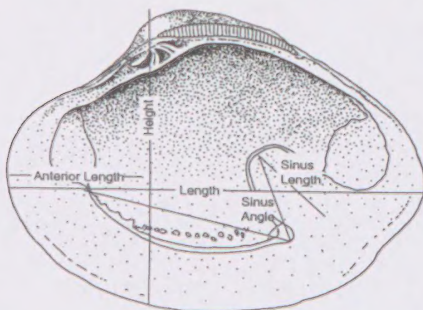


Fig. 1. Internal view of the shell of *Paphia (Protapes) sinuosa* showing the parameters used in the morphometric analyses.

METHODS

The discrimination of species based on subjective morphological analysis of shell characters is not a satisfactory method for most bivalves. In the vast Indo-West Pacific province geographic (clinal) variation can be significant and is further compounded by ecophenotypic effects. Morphometrics can add objectivity but ideally should be combined with molecular or genetic methods. This has not been possible here because of the unavailability of material. Our conclusions therefore will remain partly unsubstantiated until future research is possible.

Little attention has been given to the constancy of shell characters. In epifaunal taxa shape can be greatly influenced by spatial constriction (Seed 1980). Variation amongst infaunal bivalves is little studied but it is predictable that growth would be affected by physio-chemical conditions and food availability. Details of sculpture and external features such as the lunule and escutcheon may be less variable than shell shape. Internal anatomical features are probably more constant than shell shape or sculpture (Lam, 1980). Thus, shell characters, such as muscle scars, that reflect anatomy may be useful. In our study we place least emphasis on minor differences in shell outline, more on sculpture and most on muscle scars.

Shell measurements were made using digital vernier callipers accurate to two decimal places or from an image analyser (ImprovisionTM). These were transferred to Statview 4.0TM for statistical analyses.

Shell parameters used in the morphometric analyses are given in Figure 1. To compare measurements between species of differing shapes a standard orientation is needed. This was achieved by fixing a horizontal axis formed by the line joining the bases of the two adductor scars. Sculptural density was measured with the image analyser. The measurement used was the distance between individual concentric lirae at a fixed point on the midline below the umbo (20mm).

GENERIC DIAGNOSES

Detailed diagnoses of the genus *Paphia* are lacking, Fischer-Piette & M  t  vier (1971) concentrate on hinge characters to separate the genera within the Tapetinae. They note that the most significant character of *Paphia* is the ascending pallial sinus. The definition of an "ascending pallial sinus" is unclear, as there are considerable differences between the species

mentioned by Fischer-Piette, for example *P. gallus* and *P. cor*. There are also differences in the depth of the sinus between *P. undulata* and *P. alapapilionis*. Shell shape is also highly variable ranging from elongate/compressed in *P. alapapilionis* to subovate in *P. gallus* to rotund/ovate and inflated in *P. cor*. Sculpture varies from smooth in *P. undulata* to strongly ridged in *P. crassisulca*.

Matsukuma (1988) appears to give diagnoses for *Paphia* and *Protapes* but these refer specifically to the type species of each. As a consequence the presence of radial rows of brown spots cannot be part of the generic diagnoses as only *P. alapapilionis* has them. From his discussion however it is clear that he regarded all the short, tumid, posteriorly twisted forms as belonging to *Protapes*.

Dall (1902) erected the subgenus *Protapes* defining it on the more ovate outline and ridged sculpture. Stoliczka (1870) erected the genus *Paratapes* as a replacement for *Textrix* with the type species *V. textile* Linnaeus. Kuroda and Habe (1971) erected the subgenus *Neotapes* for *P. undulata* defining it on the short pallial sinus and weak sculpture. As *V. textile* and *V. undulata* are clearly sister species if not synonymous *Neotapes* should be regarded as a junior synonym of *Paratapes*. Considering the large amount of variation exhibited by the genus *Paphia* its definition must be rather broad.

Superfamily Veneroidea

Subfamily Tapetinae

Genus *Paphia* Röding, 1798

Type species: *Paphia alapapilionis* Röding, 1798

Tapetinae ranging in outline from elongate to roundly-subovate, compressed to tumid. Sculpture smooth, lirate or concentrically ridged. Pallial sinus ascending never confluent with pallial line, short to very deep. Subgeneric definitions can then be given as follows:—

Subgenus *Paphia* Röding, 1798

Type species: *Paphia alapapilionis* Röding, 1798

Plate 2.1–2.2. Text fig. 2

Outline elongate, with no posterior twist. Pallial sinus deep, ascending steeply. Sculpture undulating to coarsely ridged.

Subgenus *Protapes* Dall, 1902

Type species: *Venus gallus*, Gmelin, 1791

Outline subovate to roundly-subovate, with a twisted posterior ventral margin. Pallial sinus deep to very deep, ascending gently to steeply. Sculpture coarsely ridged.

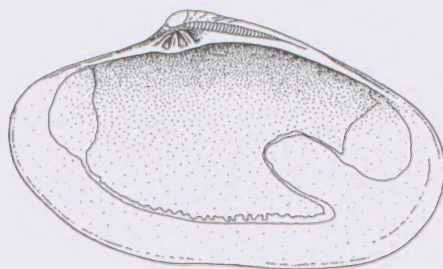


Fig. 2. *Paphia* (*Paphia*) *alapapilionis* Röding. Scale bar = 20 mm.

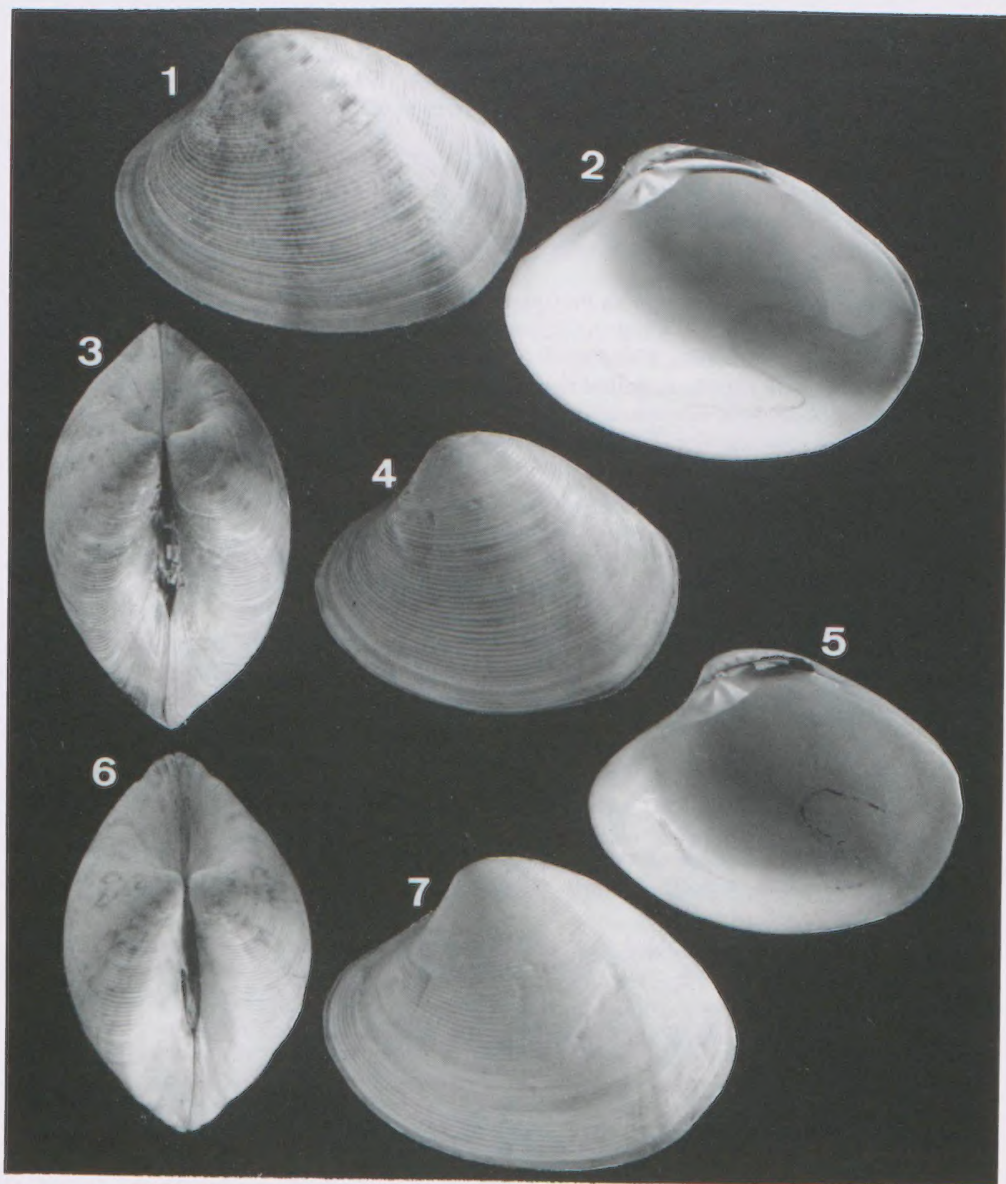


Plate 1. *Paphia (Protapes) rhamphodes* n. sp.:— 1.1–1.3, Holotype, Masirah; Figs. 1.4–1.6, Coloured specimen from Bahrain (NMW.Z. 1993.061.1295); Fig. 1.7, Large white specimen from Bahrain (NMW.Z. 1993.061.1295) All $\times 1.5$.

Subgenus *Paratapes* Stoliczka, 1870

Type species: *Venus textile*, Linnaeus, 1758

Outline elongate with no posterior twist. Sculpture smooth. Pallial sinus short, ascending steeply.

All three subgenera are present in the western Indian Ocean. *Paphia (Paphia) alapapilionis* is restricted to Madagascar, Mauritius and possibly Ceylon and only *Protapes* and *Paratapes* are found in the Arabian Sea. This paper will not consider *P. (Paratapes.) undulatus* further other than to note its widespread occurrence in the Arabian Sea and Arabian Gulf.

SPECIES DESCRIPTIONS

Paphia (Protapes) rhamphodes n.sp.

Plate 1.1–1.7. Text figs. 3a–d.

Paphia cor Sowerby: Ahmed 1975

Protapes n. sp.: Oliver in Dance, 1995, 274, fig. 1230.

Material

Holotype: 1 complete shell (37.8 mm in length \times 29.6 mm in height), Umm Rusays, Masirah, Sultanate of Oman, coll. S.P. Dance, 24.xi.1991. NMW.Z. 1993.061.1303.

Paratypes: 1 shell as holotype NMW.Z. 1993.061.1304; 2 shells as holotype NMW.Z. 1993.061.1305; 10 specimens BMNH 1995082.

Other material examined: Outer Tubli Bay, Bahrain, 20 sh., Coll H.C.G. Chesney & S. Green, xi. 1992, NMW.Z. 1993.061.1295, 1296; as above but Coll E. Glover & S. Green 1994, BM(NH); Umm al Qaywayn, United Arab Emirates, 2v. Coll. H.C.G. Chesney, Nov. 1992, NMW.Z. 1993.061. Between As Sib and Muscat 23°41'N 58°11'E to 23°37'N 58°36'E, 2sh., Coll D. Bosch, 1992, NMW.Z. 1993.061.1301; Muscat 23°37'N 58°36'E, 1sh, Coll D. Bosch, 1992, NMW.Z. 1993.061.1297; 3sh, NMW.Z. 1993.061.1302; Sur Masirah, Masirah, 20°26'N 58°43'E, 10v., Coll S. P. Dance, 23.ii.1989, NMW.Z. 1993.061.1299; 4v, 17.ii.1989, NMW.Z. 1993.061.1298; Umm Rusays, Masirah, 20°29'N 58°47'E, 1sh., Coll. S. P. Dance, 24.xi.1991.

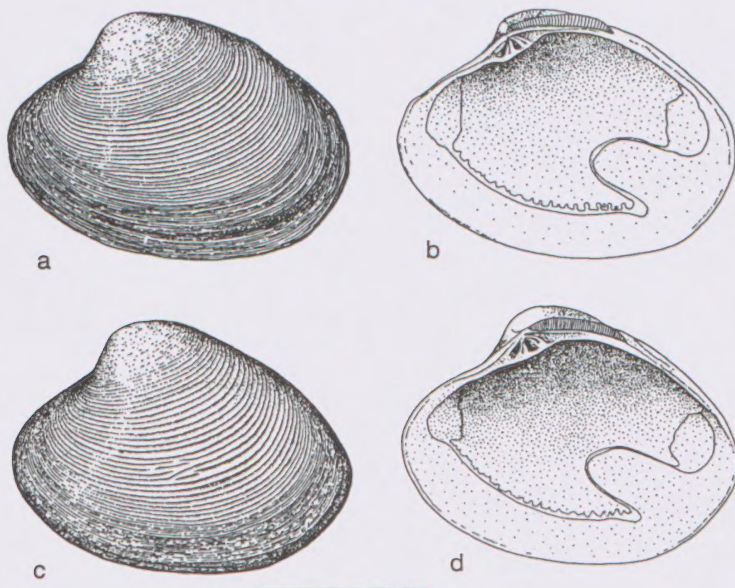


Fig. 3. *Paphia (Protapes) rhamphodes* n. sp.: a–b, typical form from Masirah; c–d, Gulf form from Bahrain. Scale bar = 15 mm.

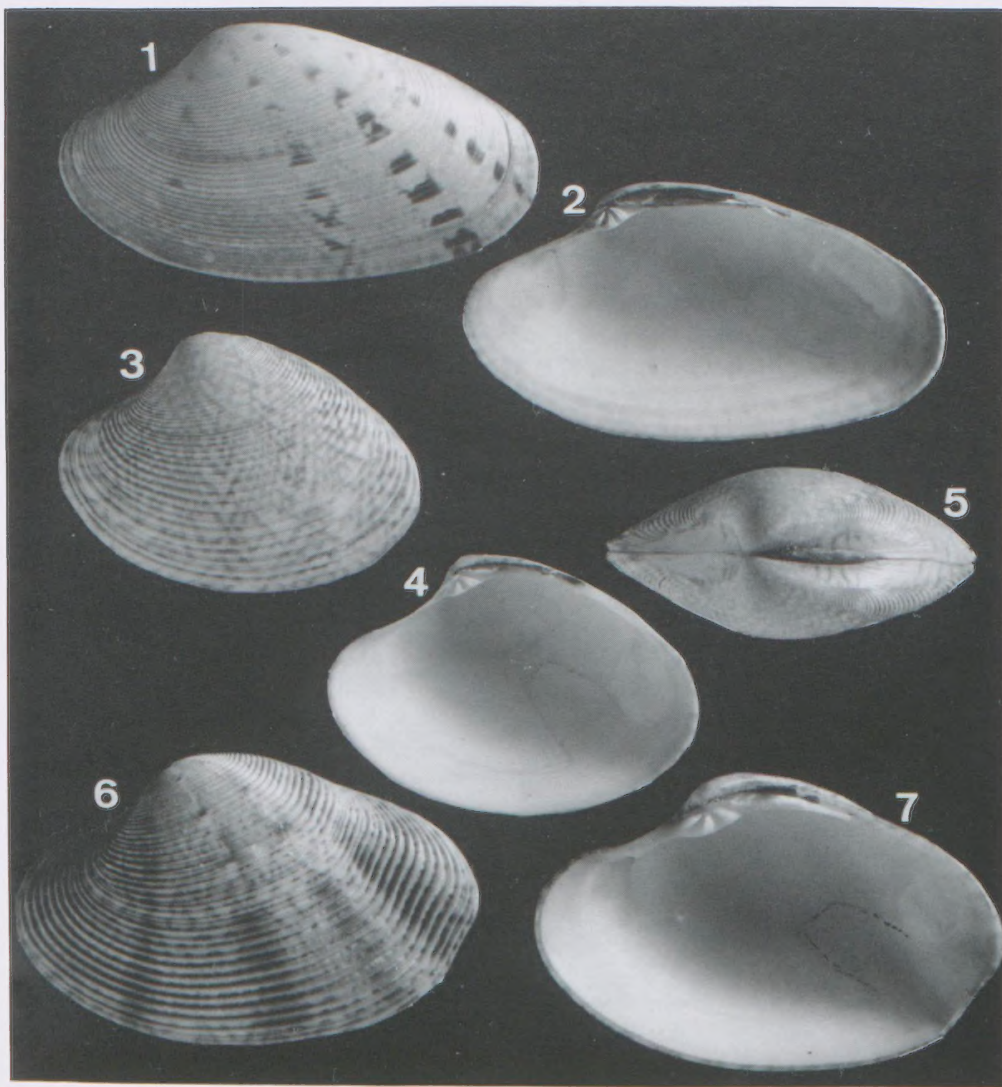


Plate 2. 2.1–2.2, *Paphia (Paphia) alapapilionis*, Indian Ocean (NMW. 1955.158) $\times 0.5$; 2.3–2.5, *Paphia (Protapes) gallus*, Singapore (NMW. 1955.158) $\times 1$; 2.6–2.7, *Paphia (Protapes) sinuosa*, Masirah (NMW.Z. 1993.061.1699) $\times 1$.

Description: Shell to 46 mm in length; shell solid but light, moderately inflated (Length to Tumidity ratio 1.74:1, range 1.55:1–1.98:1). Shell inequilateral, beaks towards the anterior (Anterior Length to Total Length ratio 3.48:1, range 3.18:1–3.82:1), sub-ovate, slightly longer than high (Length to Height ratio 1.25:1 range 1.17:1 to 1.33:1), anterior considerably narrower than posterior; posterior dorsal margin sloping gently, slightly sinuous on posterior margin, which can be sub-truncate. Ventral margin evenly rounded, anterior dorsal margin short, slightly concave, anterior margin sub-acute. Escutcheon weak, shallow, concentric sculpture fading. Lunule narrowly cordate, smooth. Sculpture fine, of

closely spaced concentric lirae (lirae spacing 0.56 mm, range 0.44–0.75). Hinge with three cardinal teeth in each valve, radiating from the beak; RV posterior and middle slightly bifid LV anterior and middle bifid anterior cardinal thin, often worn. Ligament on long, shallow nymph. Lunule margin with weak sub-marginal groove in RV. LV with longer weak sub-marginal groove. Remainder of inner margin smooth. Adductor scars with posterior slightly rounder and larger than anterior. Pallial sinus moderately deep, sub-quadrate and slightly erect (pallial sinus angle 35° , range 26° – 39°). Pallial line associated with discrete accessory pallial muscle scars. Colour background dirty greyish cream with two to four occasional broad radial rays often interrupted near umbo. Rays dull purple-brown in colour.

Shells from the Arabian Gulf, notably Bahrain, are different because of their predominantly cream or white shells. Morphometric analysis showed that they were more reduced anteriorly (Anterior Length to Total Length ratio 3.29:1 as opposed to 3.48:1, *f* test significant at $p=0.001$). The sculpture is coarser (0.66, range 0.54–0.88 as opposed to 0.56, *f* test significant at $p=0.001$).

Derivation of name: *rhamphodes* from the Greek “beaked”

Habitat: Recorded from intertidal sandy mud flats at the mid-shore level. In Bahrain a zonation of venerids is apparent (pers. obs. authors); *Circenita callipyga* occurs on the upper shore, with *P. (P.) rhamphodes* and *Amiantis umbonella* confined to mid shore but absent from the sea grass beds which are exposed at extreme low tide. They are shallow burrowers which are often dislodged and found on the surface.

Distribution: Gulf of Oman from Masirah, Muscat and Fujayrah; Arabian Gulf from Ras al-Khaymah (archaeological material only), Umm al-Qaywayn, Bahrain, Kuwait and Shatt al-Arab (Fig. 7a).

Remarks: *Paphia (Protapes) rhamphodes* n.sp. can be distinguished from *P. (P.) sinuosa* and *P. (P.) gallus* by its finer sculpture (Fig. 9A) and shallow semi-erect pallial sinus. From *P. (P.) sinuosa* further by its more rounded, more tumid and more anteriorly reduced outline (Figs. 9B–9D). *Paphia cor* differs in lacking a defined lunule, having a more spherical form and having a very short pallial sinus. All morphometric analysis of these comparisons are significant at the 95% level at *p* values greater than 0.0001. In outline and fine concentric sculpture *rhamphodes* resembles *Paphia (Protapes) irrediviva* Makiyama 1930, an extinct late Pleistocene species from Japan (Matsukuma 1988), but lacks the erect pallial sinus.

Paphia (Protapes) rhamphodes is recorded archaeologically only from Ras al-Khaymah, U.A.E. Fifteen valves were recovered from Julfar, a 13th–16th AD century settlement on a beach north of Ras al-Khaymah township, excavated in 1992. The specimens were found amongst a large collection of venerid clams in a late habitation layer of the site. The shells are evidently the remains of food. The most common species (>90%) are *Marcia* sp, with small numbers (in order of abundance) of *Amiantis umbonella*, *Callista erycina*, *P. (P.) rhamphodes*. and *Circenita callipyga*. One specimen of *P. (P.) rhamphodes* was recovered from archaeological deposits at Rafaq, Ras al-Khaymah, an inland settlement of probably late 1st millennium BC.

There are no earlier records of *P. (P.) rhamphodes* from the Arabian Gulf but the archaeological record is limited. Archaeo-zoological samples from the settlement of Saar, Bahrain, dated to 2000BC, did not contain *P. rhamphodes* although there are great numbers of other intertidal venerids including *Marcia* cf. *flammea*, *Amiantis umbonella* and *Circenita callipyga* (Glover 1995). This result is suggestive of a relatively recent appearance of *P. (P.) rhamphodes* in the Arabian Gulf.

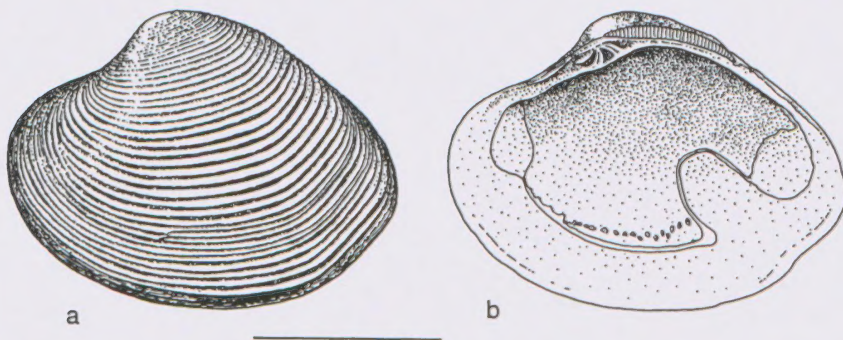
Paphia (Protapes) sinuosa (Lamarck, 1819)

Plate 2.6–2.7. Text figs. 4a–b.

Venus sinuosa Lamarck, 1818 p. 604*Tapes lentiginosus* Reeve, 1864 pl. 6 fig 25*Tapes sinuosa* Lamarck: Römer, 1870 p. 35, pl. 11 fig. 1*Paphia malabarica* (Chemnitz) part: Fischer-Piette and Métivier 1971, p. 39–41 pl. 9 figs 7–10.*Paphia (Protapes) sinuosa* (Lamarck, 1818) Matsukuma 1988 p. 413 pl. 2 figs. 3–4.*Material**Syntypes*: MNHN, Paris

Other material examined: Kalban, Masirah, 20°20'N 58°38'E, 1sh., Coll. M. Day, 9.i.1993, NMW.Z. 1993.061.1699; Masirah, 2sh., Coll. D. Bosch, NMW.Z. 1991.103; Sur Masirah, Masirah, 20°26'N 58°453'E, 3sh., Coll. S. P. Dance, 17.ii.1989, NMW.Z. 1993.061.1700; 2sh., 23.xi.1991, NMW.Z.1993.061.1705; 1sh, 22.xi.1991, NMW.Z. 1993.061.1706; 1sh., Coll. M. Day, 05.ii.1993, NMW.Z. 1993.061.1707; Umm Rusays, Masirah, 20°29'N 58°47'E, 5sh., Coll. M. Day, 6/7.ii.1993, NMW.Z. 1993.061.1701; Muscat, 2sh., Coll. D. Bosch.; Hormuz, Mussandam, 2v. Coll. K. Smythe, i.1976, NMW.Z. 1995.008.265; Rams, Ras al Khaymah, 25°45'N 55°55'E, 4sh., Coll. S. P. Dance, i.1993, NMW.Z. 1993.061.1702; Juffair, Bahrain, 1sh. + 2v., Coll. S. Green, xi.1991, NMW.Z. 1993.061.1703/4; Aden, Coll. Major Yerbury, BM(NH) 4.9.4.9; Muscat, Coll. R. Jayakar BMNH 339; Gulf of Oman, Coll. K. Smythe BM(NH) 2341; Aden, Coll. Dinshau, BM(NH); Aden, Coll. A.J. Peile, BM(NH); Malaya, Coll. R. D. Purchon BM(NH) 2264; Mozambique, Coll. P. M. Reid BM(NH) 2341; Aden, Coll. H. E. Biggs BM(NH) 2258; Tranquebar, India, 6sh., Coll. Spengler, 4sh., Coll. Vedelsby, ZMC.

Description: Shell length to 75 mm. Shell solid, slightly inflated (Length to Tumidity ratio 2:06:1, range 1:67:1–2:37:1). Inequilateral, beaking towards anterior (Length to Anterior Length ratio 2:87:1, range 2:62:1–3:03:1), sub-ovate (Height to Length ratio 1:37:1 range 1:26:1–1:48:1); posterior margin sloping gently, strongly sinuous on posterior margin, subtruncate, ventral margin slightly sinuous. Anterior dorsal concave, anterior margins subacute. Escutcheon weak, shallow, indistinct ridges. Lunule lanceolate, slightly concave, weakly ribbed. Shell sculpture strong concentric ridges (lirae spacing 1:32 mm, range 0:84–1:71) separated by nearly equal grooves. Hinge with three cardinal teeth in each valve, radiating from beak; RV posterior and middle bifid; LV anterior and middle bifid, anterior cardinal thin and often worn. Ligament shallow. Lunule margin LV with sub-marginal groove, RV sub-marginal groove weaker. Remainder of inner margin smooth. Sub-circular posterior adductor scar larger than semi-circular anterior scar. Pallial sinus deep, sub-acute,

Fig. 4a–b, *Paphia (Protapes) sinuosa* (Lk.) from Masirah. Scale bar = 25 mm.

erect (44° , range 38° – 50°), pallial line associated with accessory pallial muscle scars. Shell colour fawn with four brown rays and zigzag streaks.

Habitat: Sub-tidal soft substrates.

Distribution: Indo-West Pacific from Mozambique to southern China and Philippines (Fig. 7c.)

***Paphia (Protapes) gallus* (Gmelin, 1791)**

Plate 2.3–2.5, Text fig. 5

Venus malabarica Chemnitz, 1782: p. 323, pl. 31 figs. 324–325.

Venus gallus Gmelin 1791: p. 3277.

Tapes malabarica Chemnitz: Römer, 1870 p. 34 pl. 10 fig. 3

Paphia malabarica (Chemnitz) part: Fischer-Piette and Métivier 1971: 39–40

Paphia (Protapes) gallus (Lamarck, 1818): Matsukuma, 1988 p. 412, pl. 2 figs. 5a–b.

Material

Holotype: not located.

Other material examined: Singapore, 8sh., leg. S. Archer, Coll. Melvill-Tomlin, NMW.1955.158; Siglap, Singapore, 10sh., Coll. H. Winckworth, 11.vi.1933, BM(NH); Malabar Coast, 4sh., Coll. Melvill-Tomlin, NMW. 1955.158; Malabar Coast, 6sh., Coll. H. Cuming, BM(NH); North Queensland, Australia Coll. D. Reid BM(NH); Ennur, Coll. H. Winckworth, BM(NH) 1953 1.2; Penang, Malaysia, 4sh., Coll. H. Winckworth, 14.iii.1933, BM(NH).

Description: Shell length to 65 mm; shell solid but light, not inflated (Length to Tumidity ratio 2.15:1, range 1.57:1–2.47:1). Shell inequilateral, somewhat extended towards anterior (Length to Anterior Length 2.88:1, range 2.64:1–3.13:1), sub-ovate (Height to Length ratio 1.36:1 range 1.24:1–1.44:1), posterior margin sloping gently, straight, weakly sinuous on posterior margin. Anterior dorsal margin concave, anterior margins sub-acute. Escutcheon long, narrow, weakly striated with blunt ridge running from beak towards postero-dorsal. Lunule lanceolate, slightly concave, smooth, with indistinct shallow groove on lunule margin. Shell sculpture low concentric riblets separated by shallow narrower grooves (1irae spacing 1.05 mm, range 0.85–1.36). Hinge plate, thin, with three cardinal teeth in each valve radiating from beak; RV posterior and middle bifid; LV anterior and middle bifid, anterior cardinal thin. Inner margin smooth. Adductor scars sub-circular with posterior scar larger than semi-circular scar. Pallial sinus deep, sub-quadrate, very erect (Pallial sinus angle 52° ,

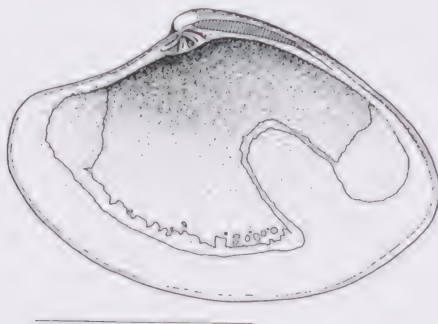


Fig. 5. *Paphia (Protapes) gallus* (Gmelin) from Singapore. Scale bar = 30 mm.

range 45°–59°). Pallial line dorsally associated with discontinuous accessory pallial muscle scars. Colour fawn, with four, more or less, distinct brown rays and/or narrow zigzag streaks.

Habitat: Sub-tidal soft substrates.

Distribution: Indo-West Pacific from Malabar coast of south-west India to Philippines and northern Australia. Apparently absent from greater part of the western Indian Ocean (Fig. 7c).

***Paphia (Protapes) gallus bombayana* n. subsp.**

Plate 3.1–3.3, Text fig. 6

Material

Holotype: Ratnagiri, 1sh., leg. Aitken, Coll. A. J. Peile, BM (NH) 996023.

Paratypes: Ratnagiri, 2sh., leg. Aitken, Coll. A. J. Peile, BM(NH) 2242; Bombay, 2sh. Leg. Abercrombie, Coll. Melville-Tomlin, NMW.1955.158.

Other material examined: Bombay, 4sh., Coll. H. Winckworth, 1.v.1945, BM(NH). 1953.1.2.169–172; Bombay, 6sh., Coll E. Deakin BM(NH) 1909.9.23 1–6; Karwar, Coll. H. Winckworth, 24.ii.1944, BM(NH) 1953. 1.2.173; Khar Beach, Bombay, 3sh. + 1v., Coll P. Narang viii. 1969, BM(NH); Karachi, 1 sh., Coll. A. Salisbury, BM(NH) 2172;

Description: Shell length to 75 mm; shell solid, inflated (mean Length to Tumidity ratio 1.79:1, range 1.61:1–2.00:1). Inequilateral, beaking towards the anterior (Length to Anterior Length ratio 3.04:1, range 2.69:1–3.49:1), sub-ovate (Height to Length ratio 1.23:1 range 1.16:1–1.30:1, anterior narrower than posterior; posterior margin sloping gently, slightly convex. Slightly sinuous on posterior ventral margin. Anterior dorsal margin concave. Escutcheon long, narrow, striated. Lunule broad, lanceolate, slightly concave smooth with indistinct shallow groove on lunule margin. Sculpture of concentric ribs separated by distinct grooves in adult (lirae spacing 1.11 mm range 0.86–1.39). Hinge plate fairly narrow with three cardinals in each valve radiating from beak; RV posterior and middle bifid; LV anterior and middle bifid. Inner margin smooth. Adductor scars sub-circular with posterior scar larger than semi-circular anterior scar. Pallial sinus deep, sub-quadrate very erect (Pallial sinus angle 47°, range 33°–56°) Pallial line with discontinuous

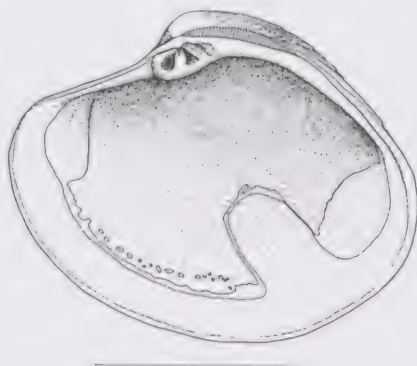


Fig. 6. *Paphia (Protapes) gallus bombayana* n. subsp. from Bombay. Scale bar = 30 mm.

accessory pallial muscle scars. Colour fawn occasionally with brown rays and/or zigzag streaks.

Habitat: Unknown.

Distribution: Eastern Arabian Sea from Karachi to Bombay (Fig. 7d).

Remarks: This variety bears a strong resemblance to the shell figured in Reeve (1864) and labelled as *Tapes turgidula* Deshayes. The true *T. turgidula* of Deshayes is synonymous with *T. turgida* Lamarck 1818.

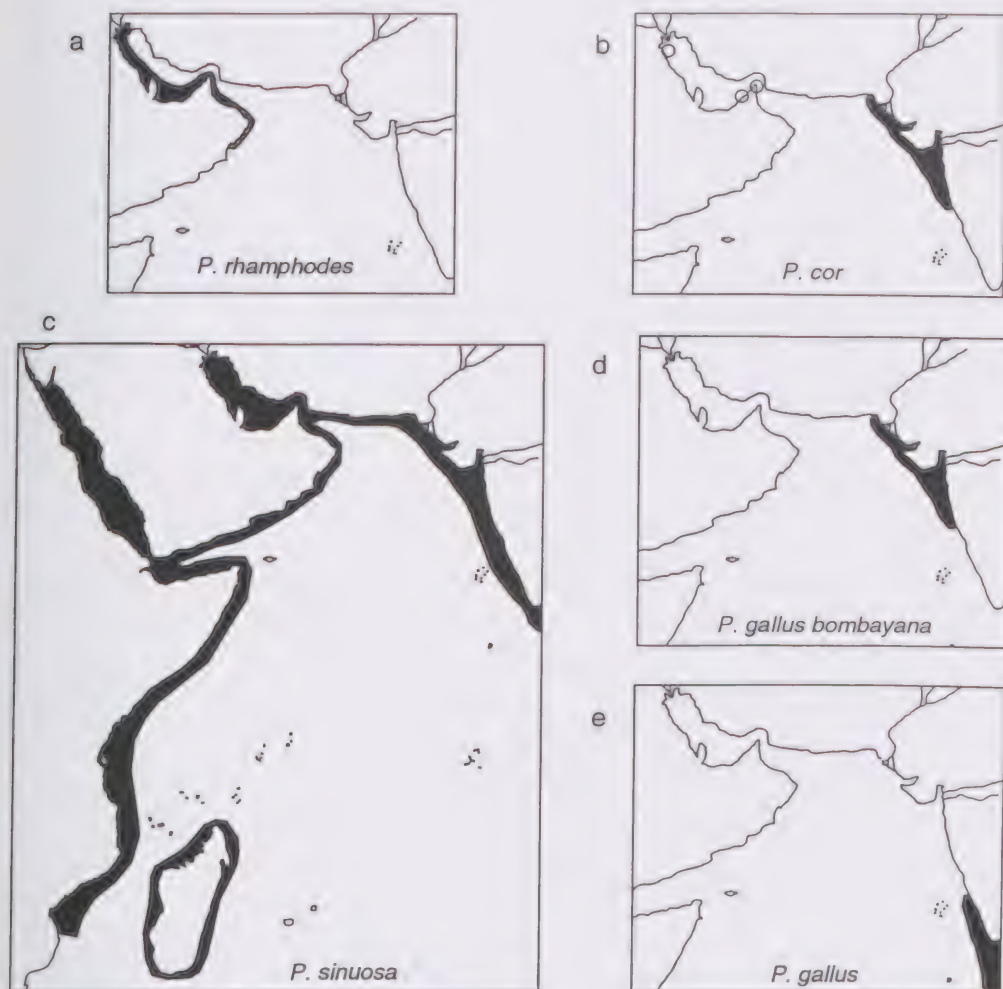
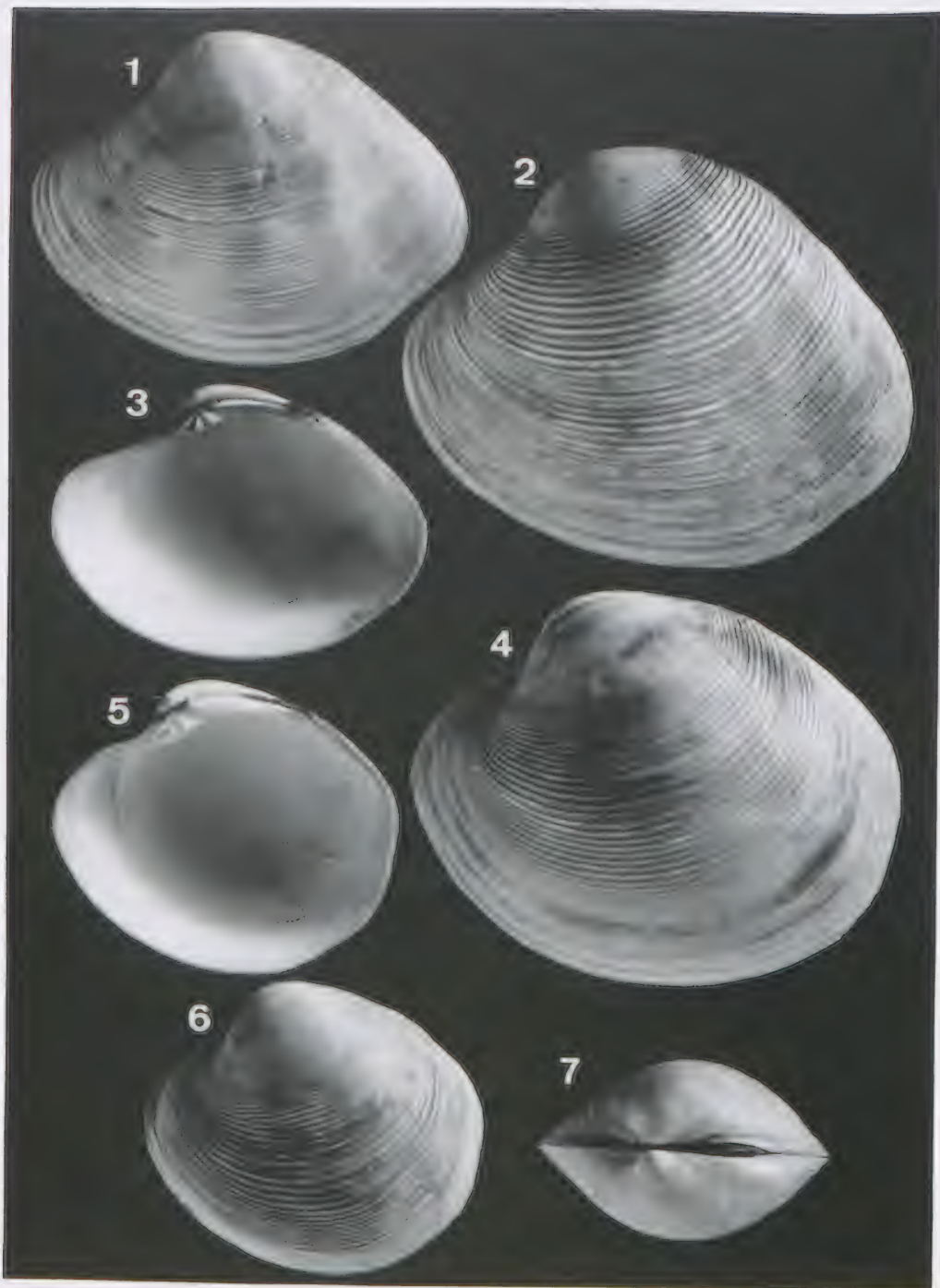


Fig. 7a-e, Distribution maps for five forms of *Protapes* found in the western Indian Ocean. Black areas - living; Open circles - dead shells only.



***Paphia (Protapes) cor* (Sowerby, 1853)**

Plate 3.4–3.77. Text figs. 8a–b.

Venus cor G. Sowerby 1853: p. 727 pl. 160 fig. 184

Tapes cor Sowerby: Römer, 1870 p. 103 pl. 40 fig. 4

Paphia cor Sowerby: Fischer-Piette & Métivier, 1971: p. 39.

Material

Holotype: BM(NH), Coll Mus. Cuming, Karachi.

Other material examined: Gulf of Kutch, 4sh. + 1v., Coll. H. Fedden, NMW. 1894.15; Baba Island, Karachi, 3sh., Leg. H. Winckworth, 6.x.1928, Coll. Melvill-Tomlin, NMW. 1955.158; 10sh., Coll. Winckworth, BM(NH) 1838; Dubai, 2v., Coll. H. Kauch, NMW.Z. 1993.061.1708; Hormuz, 1v., Coll. K. Smythe, NMW.Z. 1995.008.266; Arrakan, Burma, 2sh., Coll. H. Fedden, NMW. 1894.15; Pondicherry Coll. McAndrew BM(NH).

Description: Shell length to 75 mm; shell relatively solid, well inflated (Length to Tumidity ratio 1.50:1, range 1.36:1–1.62:1). Inequilateral, beaking towards anterior (Length to Anterior Length ratio 3.34:1 range 3.13:1–3.52:1). Shell broadly sub-ovate; anterior narrower than posterior, posterior dorsal margin rounded somewhat sinuous on posterior margin, which can be sub-truncate. Ventral margin well rounded; anterior dorsal margin short, concave, anterior margin sub-acute. Escutcheon very weak, shallow, ribbed. Lunule indistinct, ridged. Shell sculpture of many strong, concentric ridges separated by nearly equal grooves (lirae spacing 0.74 mm, range 0.52–1.01). Hinge with three cardinal teeth in each valve; RV posterior and middle bifid; LV anterior and middle bifid; anterior cardinal thin, curved. Ligament on long shallow nymph. Lunule margins with shallow groove; remainder of inner margin smooth. Adductor scars, posterior sub-circular larger than semi-circular anterior. Pallial sinus fairly deep, only slightly erect, sub-truncate (angle 24°, range 16°–30°). Occasional accessory pallial muscle scars. Colour light fawn, slightly darker near umbo. No rays.

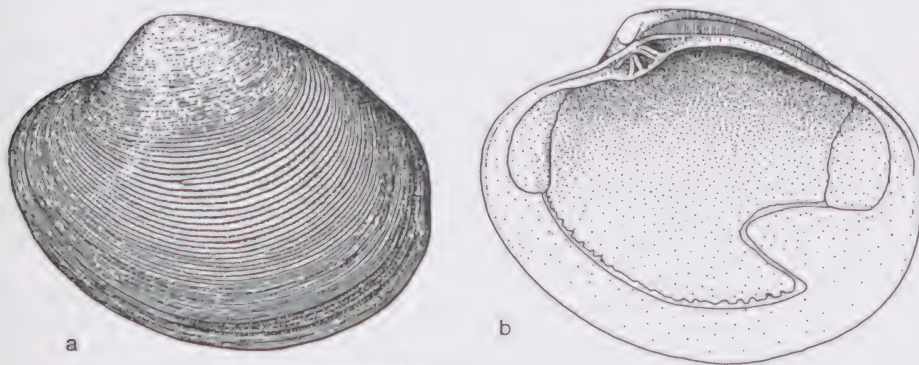


Fig. 8. *Paphia (Protapes) cor* (Sow.) from Karachi. Scale bar = 30 mm.

Plate 3. 3.1 & 3.3, *Paphia (Protapes) gallus bombayana* n. subsp. Bombay (BM(NH) 1953.1.2.169/70; 3.2, *Paphia (Protapes) gallus bombayana* n. subsp. Holotype Ratnagiri (BM(NH) 996023; 3.4, *Paphia (Protapes) cor*, Karachi (NMW. 1955.158); Figs. 3.5–3.7, *Paphia (Protapes) cor*, Arrakan (NMW. 1894.15)

Habitat: Unknown but locality data suggests that it is restricted to estuarine or brackish embayments.

Distribution: Eastern Arabian Sea from Karachi to the Gulf of Kutch and as dead shells from Kuwait and Hormuz in the Arabian Gulf (Fig. 7b) and Bay of Bengal (Pondicherry and Arrakan).

DISCUSSION

The morphometric analyses presented here give statistical credence to our conclusion that there are five separate morphological groups within *Protapes* in the western Indian Ocean. These can be distinguished on a combination of shell characters; outline as expressed by the ratios of length to height, anterior length to total length and length to tumidity; pallial sinus length and angle of ascent and external sculpture. Comparisons of these parameters are illustrated by the box plots in Figure 9A-F and the bivariate scattergrams in Figure 10.

Paphia (Protapes) cor is the most divergent and separates on nearly all characters. It is the most rounded, most tumid, has the shallowest pallial sinus and with the least angle of ascent. The posterior twisting is very slight and the lunule is not defined. The latter characters bring into doubt the placing of this species in *Paphia* s.l. In museum collections the genus *Hemitapes* is often given for *cor* but this is not correct as this name is a synonym of *Marcia* (Dall, 1902). We are reluctant without a much wider ranging review of the Tapetinae to give an alternative generic placement and follow Fischer-Piette & M  tivier in retaining it in *Paphia*.

Paphia (Protapes) rhamphodes is distinguished by its small size, fine sculpture, relatively shallow pallial sinus and the narrow beaked anterior area. The statistical significance of these characters in comparison to *P. (P.) gallus* and *P. (P.) sinuosa* are very high, all above the 95% confidence limits.

The remaining groups, described above as *P. (P.) sinuosa*, *P. (P.) gallus* and *P. (P.) gallus bombayana* all show more overlap in the morphometric analyses. *Paphia (Protapes) sinuosa* can be separated from *P. (P.) gallus* because of its shallower and less acute pallial sinus and the coarsest sculpture of all in the *Protapes* species discussed here.

Although colour is seldom reliable all *P. (P.) sinuosa* from the Arabian Sea show some radial maculations in shades of brown over a buff background. *Paphia (Protapes) gallus* is recognisable by its compressed, approximately triangular outline with a very deep, steeply ascending pallial sinus. *Paphia (Protapes) sinuosa* and *P. (P.) gallus* can be regarded as separate species as there is considerable overlap in their geographic range without any indication of intermediate forms. Neither clinal nor ecophenotypic variation are plausible explanations for the morphometric differences expressed by these taxa. This conclusion is in keeping with that of Matsukuma (1988) but conflicts with Fischer-Piette & M  tivier (1971) who synonymised these names.

Paphia (Protapes) gallus bombayana n. subsp. described here is problematic not only in terms of its relations but also because it highlights the frailty of relying on shell morphometrics alone. It is distinguishable from typical *P. (P.) gallus* primarily by its large size, more triangular outline, increased tumidity and coarse sculpture and may be equivalent to some of the monstrose forms described by R  mer (1870). The form lies at the extreme western end of the range of *P. (P.) gallus* s.l. and apparently does not overlap with the typical form which does not extend beyond the Malabar coast. We have little habitat data for this subspecies but we can note that there is an increasing influence of freshwater run off as one moves north culminating at the Indus Delta. Both clinal and ecological barriers are therefore possible explanations for the appearance of this variety. Those characters which reflect internal

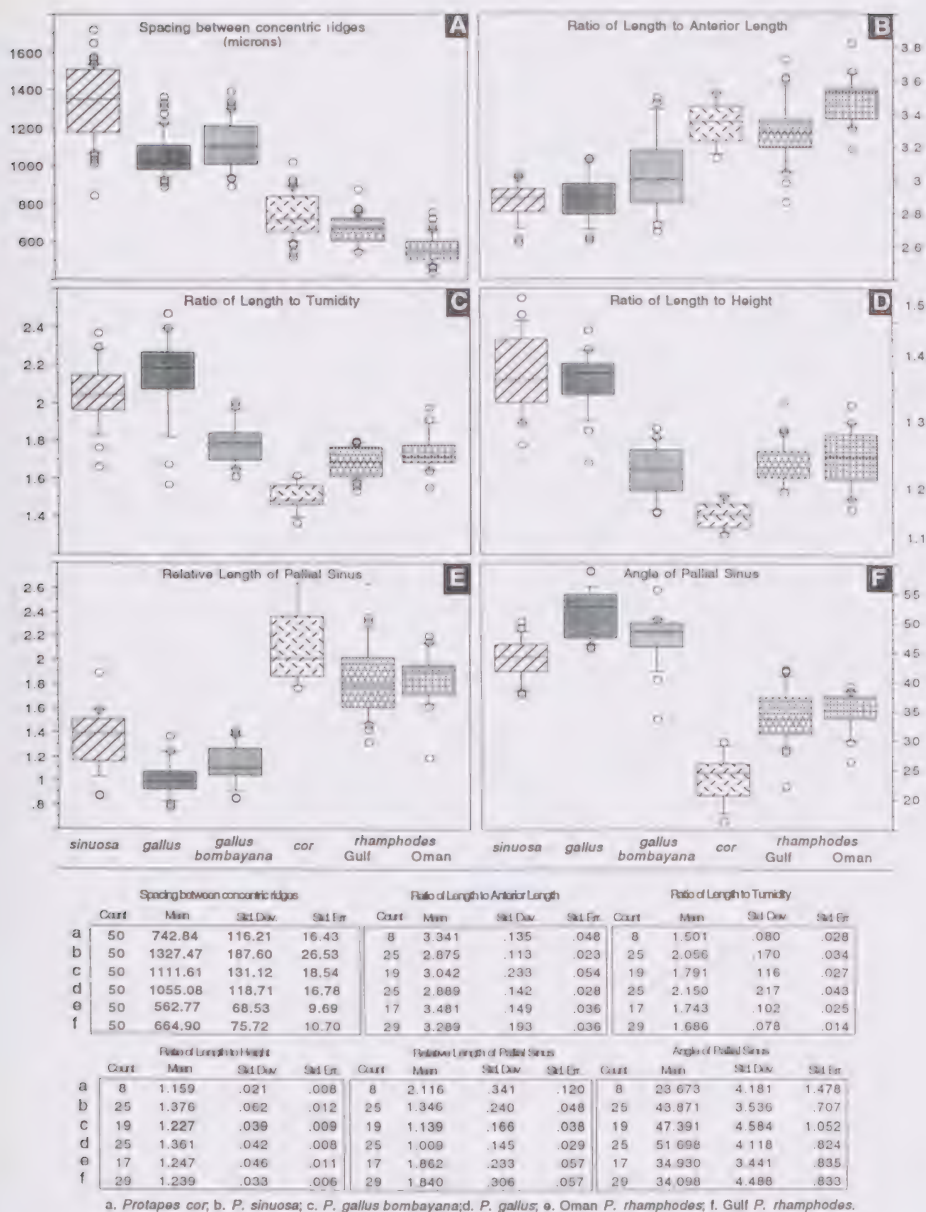


Fig. 9a-f, Box plots for comparison of morphometric analyses of six shell characters in *Protapes* from the Indian Ocean.

anatomy such as pallial sinus angle and length are not significantly different from the typical *gallus* and therefore we are reluctant to assign full species status to this morphological group without further study.

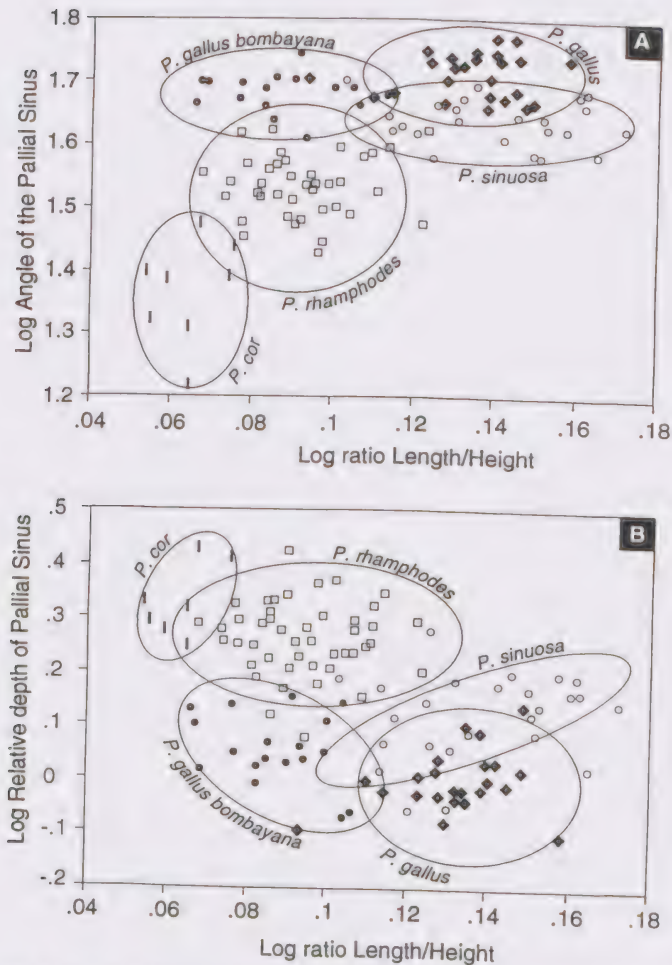


Fig. 10. Bivariate plots of outline (Length to Height Ratio) and pallial sinus characters (Angle and Depth) for five forms of *Protapes* from the Indian Ocean.

INSTITUTIONAL ABBREVIATIONS

BM(NH): British Museum (Natural History) now Natural History Museum
 NMW National Museum of Wales before 1970
 NMW.Z. National Museum of Wales after 1970
 MNHN Museum of National d'Histoire Naturelle, Paris
 ZMC Zoological Museum, Copenhagen

ACKNOWLEDGEMENTS

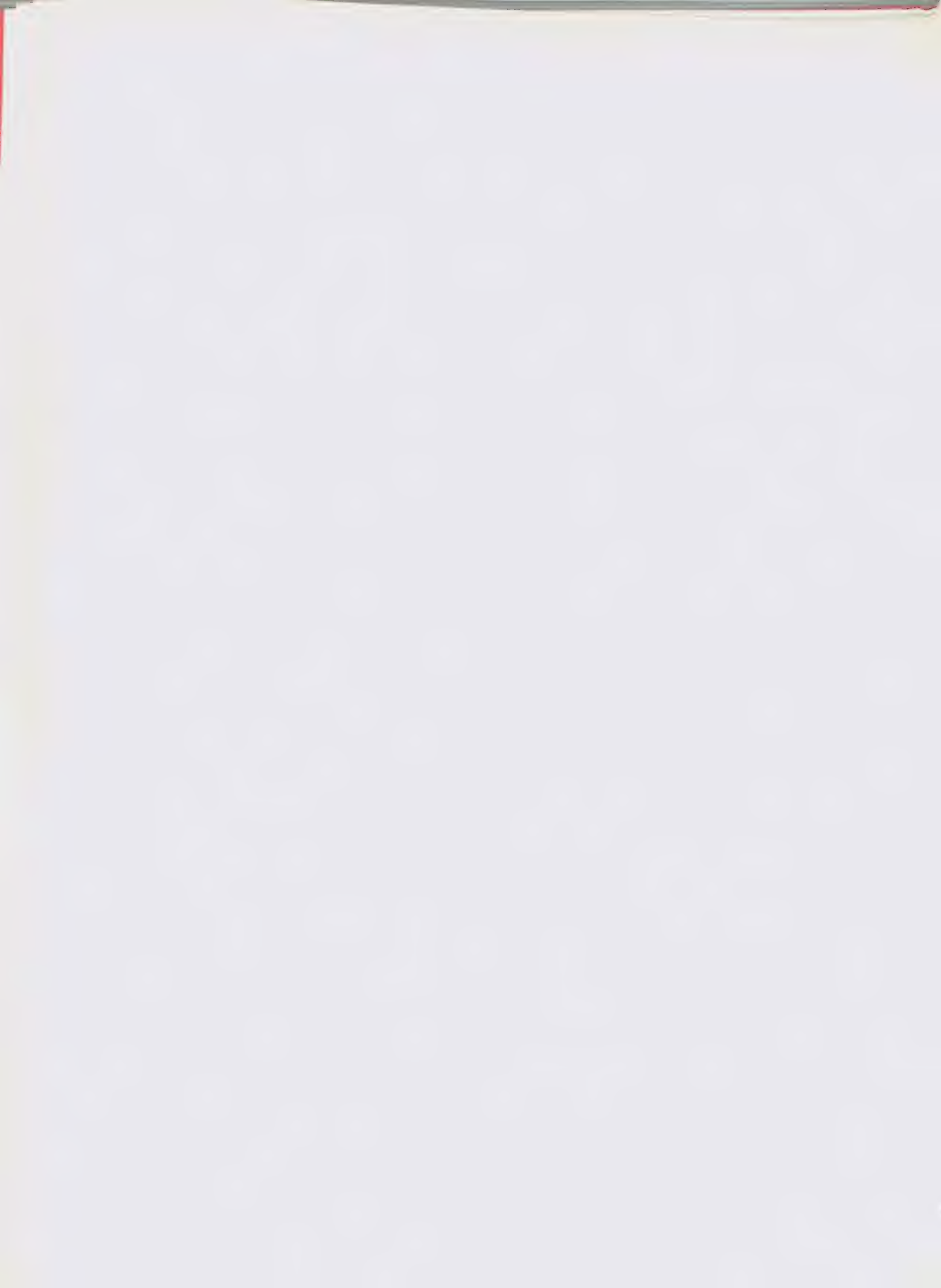
We would like to thank Steven Green for his enthusiastic interest and efforts in providing material from Bahrain. Also Don Bosch, Horst Kauch, Martyn Day and Peter Dance for

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A COLLECTION OF OPISTHOBRANCH MOLLUSCS FROM THE PITCAIRN ISLANDS¹

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(Accepted for publication, 10th February, 1996)

Abstract: Opisthobranch molluscs collected during the Sir Peter Scott Commemorative Expedition to the Pitcairn Islands (1991-2) are described. Twenty taxa were discovered from the four islands that form the group, and a further two species had been found during earlier work. The records of *Phyllobranchillus orientalis* and *Peltdoris fellowsi* represent considerable extensions to their known ranges. A large dendrodorid, provisionally referred to *Dendrodoris tuberculosa*, appears to represent the largest known specimen from this family. One new species (*Bornella irvingi*) from Ducie Atoll is described here for the first time.

Key words: Pitcairn Island, Henderson Island, Oeno Atoll, Ducie Atoll, nudibranchs, opisthobranchs, *Bornella irvingi*

INTRODUCTION

The Pitcairn Islands are of particular biogeographical importance because of their remoteness, contrasting physiographies and peripheral location at the easternmost limit of the Pacific Plate. They lie south of the Tropic of Capricorn towards the southeastern edge of the Indo-West Pacific province, some 390 km east of their nearest neighbour, Temoe Atoll in the Tuamotu-Gambier Islands, and 1570 km west of Easter Island and Sala y Gomez on the Nazca Plate. The four islands that comprise the Pitcairn Group differ markedly in physiography. Ducie and Oeno are small atolls of very different character. Pitcairn, the only island in the group still inhabited, is volcanic and has steep cliffs but very little reef development, whereas Henderson is an uplifted atoll with moderate reef development.

This paper describes the opisthobranch molluscs collected by one of us (RCP) during the penultimate phase of the Sir Peter Scott Commemorative Expedition to the Pitcairn Islands between 1991-2 (Anon. 1992). All the material has been deposited in the University Museum of Zoology, Cambridge (UMZC).

SAMPLING SITES

Details of the sampling sites are listed below for each island. All the nudibranchs were found alive in the field and were obtained by diving. The majority of shelled taxa were extracted from sediment samples sent back to Britain for laboratory analyses, although a few were also found living in the intertidal zone. In the systematic descriptions, "field notes" refer to notes made in the field by Mr Robert A. Irving, a diver on the expedition.

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Ducie Atoll (24°39'S 124°48'W). Ducie is a small atoll just over 2 km in diameter, with one larger (Acadia) and three smaller islets surrounding a central lagoon up to 15 m deep. It is not only the easternmost island on the Pacific plate but also the southernmost atoll in the world. The marine habitats of Ducie have been described by Rehder & Randall (1975) and Irving (1995). Sands and fine sediments are scarce on the fore reef and reef flat of Ducie and this is reflected in the composition of the Acadia motu, which consists almost entirely of coral rubble and shells (mostly *Turbo argyrostomus*). Cemented slabs of coral limestone were also common. Sediment samples were collected from the beaches on both the lagoon and seaward side of the motu but no opisthobranchs were found.

Henderson Island (24°22'S 128°20'W). Henderson is the largest island in the group with an area of 37 km². It is an uplifted atoll with a peripheral ridge, reaching about 30 m high, encircling a flat central basin about 22 m above sea-level, representing the site of the former lagoon. The uplift of Henderson is thought to have been relatively recent (less than 1 Myr) and has been attributed to lithospheric flexure around Pitcairn (Blake 1995). Descriptions of the modern reefs of Henderson are given by Spencer & Paulay (1989) and Irving (1995). In contrast to Ducie, the fore reef on Henderson is relatively narrow, has abundant soft sediments and supports low coral cover. Irving (1995) estimated the live coral cover on the fore reef to be 10–30%, although at sites off the east coast it reaches 80%. Adjacent to the North, North-west and East Beaches there is an extensive reef flat platform, from 40–90 m wide, between the low tide mark and the reef margin. At high tide the flat is covered to a depth of about 1–1.5 m. At low tide large areas of smooth, sand-scoured reef pavement are exposed, with well developed 'spur and groove' topography (Irving 1995). All of the Henderson material described here was collected from the vicinity of the three beaches.

Oeno Atoll (23°56'S 130°45'W). In contrast to Ducie, Oeno is located at the western end of the group and is larger, just over 4 km in diameter, and consists of a small central island surrounded by a lagoon and a fringing reef. The lagoon is shallow throughout (1.5–3 m) and has an undulating bottom of rubble and sand with scattered reefs (Devaney & Randall 1973, Irving 1995). All the shelled material from Oeno studied here was collected on the spit, now joined to the principal motu; the nudibranchs were collected in the lagoon.

Pitcairn Island (25°04'S 130°06'W). Pitcairn is a high (330 m), small (4.5 km²), volcanic island that rises precipitously from the ocean. It formed between 0.46–0.93 Myr ago (Duncan *et al.* 1975), and is the southernmost island in the group. Unlike the other islands, it lacks substantial reef development. The coral reefs that do exist are small, isolated and generally confined to depths of over 20 m. A brief description of the underwater topography and habitats of Pitcairn are given by Devaney & Randall (1973). All the material from Pitcairn studied here was collected from the beach at Down Rope.

SYSTEMATIC ACCOUNT

Order Bullomorpha (Cephalaspidea)

A very large number of species of bullomorph have been named from the Indo-Pacific region, many based on rather few shells. For most of these there has been no recent attempt to compare related species and to rationalise them by synonymy, so identification of material presents a major problem. For the bullomorphs in this collection, with one exception, only empty shells were found. These have been compared with material in the Natural History Museum (London) and their identification is either to genus or to a most likely species denoted by *cf.*

Family Acteonidae
Pupa cf. *solidula* (L., 1758)
(Fig. 1)

Material: Oeno Atoll, 1 shell.

Discussion: This species is known from both Indian and Pacific Oceans from as far west as South Africa (Macnae 1962, Gosliner 1987).

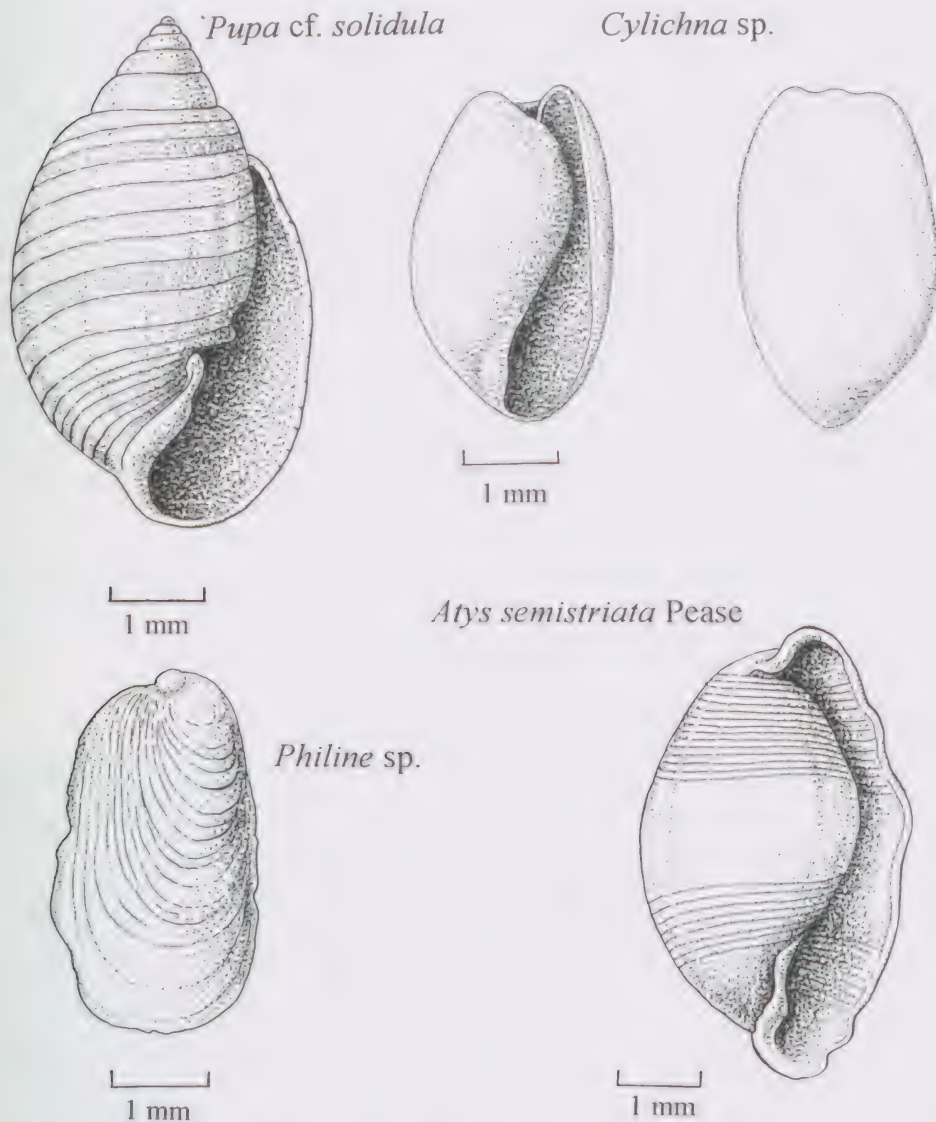


Fig. 1. Shells of *Pupa* cf. *solidula* Oeno; *Cylichna* sp. Oeno, *Philine* sp. Henderson (East Beach) and *Alys semistriata* Pease Henderson (NW Beach).

Family Cylichnidae

Cylichna sp.

(Fig. 1)

Material: Oeno Atoll, 1 shell.

Discussion: It is quite impossible to determine which of the numerous Pacific species of *Cylichna* this single shell belongs to.

Family Philinidae

Philine sp.

(Fig. 1)

Material: Henderson Island, 4 shells from sediment collected in 12 m water-depth off the East Beach.

Discussion: Identification of small *Philine* without notes on colour of the live animal is almost impossible.

Family Bullidae

Bulla cf. *punctulata* A. Adams, 1850

Material: Oeno Atoll, 6 shells (det. E. A. Kay).

Discussion: These shells are too poorly preserved to be worth illustrating, but they probably belong to the widespread species *Bulla punctulata* which occurs both in Hawaii to the west and the Galapagos Islands to the east (Sphon & Mulliner 1972). Paulay (1989) has already reported *Bulla* cf. *punctulata* from Henderson Island, so its occurrence at Oeno Atoll is to be expected. Willan (1978) has attempted a synonymy of three species of Pacific *Bulla*, but unfortunately these do not include *B. punctulata*.

Bulla sp.

(Fig. 2)

Material: Oeno Atoll, 9 shells.

Discussion: These shells clearly belong to a different species to the previous ones, but we cannot identify them further. Material that may be the same species has been described by Paulay (1989) from Henderson Island as *Bulla* sp.

Family Smaragdinellidae

Smaragdinella calyculata (Broderip & Sowerby, 1829)

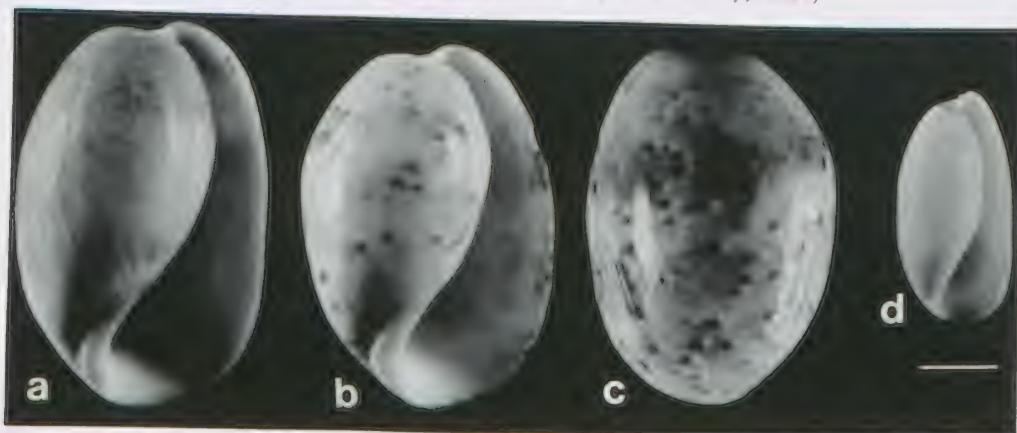


Fig. 2. Shells of *Bulla* sp. (a-c) and *Alys cylindricus* Helbling (d) from Oeno Atoll. Scale bar = 5mm.

Material: **Henderson Island**, 21 specimens close to High Water mark on the reef flat of the North Beach, 23.12.1991; 1 shell at East Beach. **Pitcairn Island**, 2 shells at Down Rope.

Description and Discussion: Field notes describe the living animals as "small green bullomorph-type slugs". The preserved animals are still green and very much contracted, but the soft parts still project anteriorly one or two millimetres beyond the shell. Much of the green pigment has dissolved out in the ethanol preservative. The shells range from 5.0 to 6.3 mm length and are yellow-brown. The animals are very shrunken so that few external features typical of bullids are visible. Nevertheless they resemble the description given by Marcus & Burch (1965) from Eniwetok Island. This herbivorous species commonly lives on exposed rock faces; this habit and other aspects of its functional morphology have been described by Rudman (1972).

Family Haminoeidae

Atys cylindricus Helbling, 1779

(Fig. 2)

Material: **Oeno Atoll**, 26 shells. **Henderson Island**, 4 shells at East Beach.

Discussion: This species occurs throughout the Pacific and Indian Oceans as far west as South Africa (Gosliner 1987). The shell is illustrated by Wells & Bryce (1993).

Atys semistriata Pease, 1860

(Fig. 1)

Material: **Henderson Island**, 1 shell at North-west Beach. **Oeno Atoll**, 1 shell.

Discussion: A live specimen of this species has recently been illustrated from Western Australia by Wells & Bryce (1993). It is known from the Red Sea to Hawaii (Heller & Thompson, 1983).

Haminaea sp.

(Fig. 3)

Material: **Henderson Island**, 4 shells at East Beach.

Discussion: Species of *Haminaea* are most easily identified by colour markings of the living animal.

Family Retusidae

Retusa sp.

(Fig. 3)

Material: **Oeno Atoll**, 5 shells.

Discussion: These shells are similar to *Acteocina sandwicensis* Pease, figured by Kay (1979, fig. 137N) but they did not match the lectotype of this species (BM1962751).

Order Thecosomata

Family Limacinidae

Limacina bulimoides (d'Orbigny, 1836)

Material: **Oeno Atoll**, 1 shell (det. A. W. Janssen).

Limacina lesueuri (d'Orbigny, 1836)

Material: **Henderson Island**, 2 shells in sediment from 12 m water-depth off the East Beach (det. A. W. Janssen).

Order Sacoglossa

Family Juliidae

Julia exquisita Gould, 1862

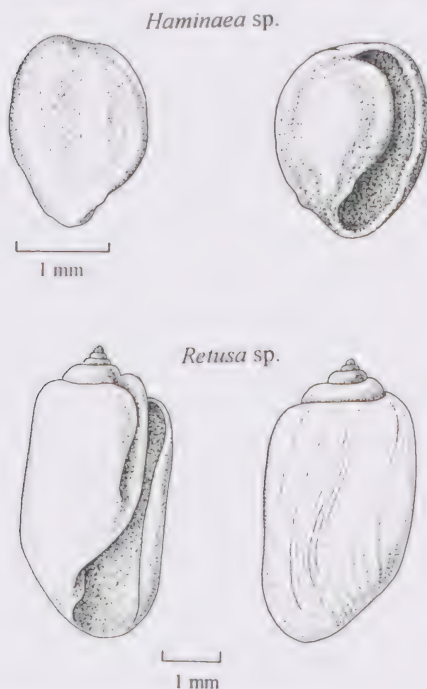


Fig. 3. Shells of *Haminaea* sp. Henderson (East Beach) and *Retusa* sp. Oeno.

Material: **Henderson Island**, 3 shells from East Beach; 12 shells from North-west Beach. **Oeno Atoll**, 7 shells. **Pitcairn Island**, 5 shells from Down Rope.

Discussion: This was the first bivalved gastropod of the genus *Julia* to be found alive (Kay 1962), and since it has been reported further east at Easter Island (Rehder 1980), its occurrence here was to be expected. It feeds on green algae in shallow water.

Family Caliphyllidae

Phyllobranchillus orientalis (Kelaart, 1858)

Material: **Oeno Atoll**, 1 specimen under a stone on the reef crest from 1 m depth on the North-western reef, 6.11.1991.

Description and Discussion: Field notes describe the live animal as having "sticky green leaf-like cerata on the back". The preserved animal is 13 mm long, all pigment having dissolved out. It is creamy white with numerous white glands visible on the cerata. Its external features agree well with those described from Japan by Baba & Hamatani (1971), and it lacks the metapodial groove characteristic of the otherwise very similar genus *Cyerce*. There are several synonyms for this species (summarised by Baba & Hamatani 1971), although there has been no recent rigorous study of specimens from different parts of its geographical range to confirm that they are all conspecific. It occurs from East and South Africa, India and Ceylon (Sri Lanka) to New Caledonia, Hawaii, and the Caroline Islands [Eliot 1904, Alder & Hancock 1864 (as *Phyllobranchus orientalis*), Kelaart 1859 (as *Proctonotus orientalis*), Bergh 1905 (as *Phyllobranchus rubicundus* and *P. prasinus*), Risbec 1953, Pease 1866 (as *Lobifera papillosa*), Marcus 1965 (as *Phyllobranchillus prasinus*), Gosliner 1988], but this is the most easterly record to date.

Order Nudibranchia
 Suborder Doridacea
 Family Dorididae

Peltodoris fellowsi Kay & Young, 1969

Material: **Henderson Island**, 1 specimen with an egg ribbon under a stone on the reef flat of the North Beach, 9.10.1991; 1 specimen on the seaward side of the reef crest at 0.5 m depth, 21.12.1991.

Description: Field notes together with a photograph show that the living animals were white, with the rhinophore clubs and gill tips black, and with black ocelli on the notum. The black is retained in the preserved specimens which measure 12 and 14 mm in length (the larger one is reflexed so this measurement is approximate). The bases of both rhinophores and gills are retracted into sockets so are not visible. It is not possible to count the rhinophore leaflets without dissecting the specimens, but the smaller animal has five small gills, four black and one of the posterior gills white. The gills are irregularly one- or two-pinnate with rather few small pinnae. The mantle is densely covered with evenly sized small, low, rounded tubercles. The foot is bilabiate and the oral tentacles are digitiform. The genital opening is easily seen so these animals may have been sexually mature.

Discussion: This material is very similar to that described by Kay & Young (1969), but their description is based on a 40 mm long animal. A 30 mm specimen is illustrated in colour by Bertsch & Johnson (1981), and the colour photographs of our material clearly show that it is the same species. The colour is similar to that of *Chromodoris sibogae*, but *P. fellowsi* differs in having a broader body with minute tubercles and in lacking a gold rim to the mantle.

This is the first record of this species from outside the Hawaiian Islands.

Unidentified dorid

Material: **Henderson Island**, 1 specimen on North Beach, 9.10.91.

Description and discussion: The specimen was pale green alive, and is 7 mm long preserved, white, with minute granular tubercles on the mantle. There are a score of dorid species to which this specimen could belong, and as it is very likely immature with no obvious external characteristics we have not attempted to identify it further.

Family Dendrodorididae

Dendrodoris tuberculosa (Quoy & Gaimard, 1832)

(Fig. 4)

Dendrodoris tuberculosa (Quoy & Gaimard); Preece 1995: p. 358.

Material: **Henderson Island**, 1 specimen at 12 m depth on North Beach, 7.12.1991 (UMZC reg. no. I 21757). It was in a large hole on the reef with only the gills visible.

Description: A detailed sketch and colour photographs of the living animal are available (Fig. 4). The notum is greyish brown with the gills a darker chocolate, but tipped with white. The pleated edge of the mantle is white. The ventral surface of the foot, mantle and head are all whitish. The compound tubercles on the notum carry many nipple-like projections.

The preserved animal is 220 mm long and 170 mm broad. The mantle edge is thin and extremely convoluted. The notum has four large raised warts medially between the rhinophores and the gills, each wart carrying a ring of small nipple-like projections surrounding a denser cluster of similar pustules. There are four similar large raised warts on each side of this medial group, with additional warts in front of the rhinophores and behind the gills. Lateral to these warts are about ten smaller compound pustules on each side, and there are still smaller raised clusters of small papillae at the base of the thin, corrugated mantle edge. The rhinophores are about 25 mm long with the perfoliate club 15 mm anteriorly, rather less posteriorly. There are at least 30 perfoliations with an anterior medial groove and a posterior ridge. One of the rhinophores is deformed with a bifid club. The



Fig. 4. *Dendrodoris tuberculosa* (Quoy and Gaimard). Dorsal view of live animal, drawn from a colour slide and a sketch by Robert Irving, together with details added from preserved specimen. Length 220 mm preserved, so probably c250 mm live.

rhinophores emerge from 5 to 6 mm thin, cylindrical sheaths. The gills are so complex that it is exceedingly difficult to distinguish the main rhaches from the principal pinnae; there could be just five gills, or there could be 14. However, since the gill opening has five deep indentations, it is probable that the true number of gills is five. They are three to four pinnate and in the preserved animal measure 100 mm across.

The foot has a thin lateral border that is almost as convoluted as the mantle edge. There are two minute oral tentacle ridges, as in other dendrodorids, and a thin, cylindrical proboscis projects from the mouth. It is 20 mm long and 3 mm diameter with a narrow transverse ridge half way to the mouth, and it tapers to a point anteriorly.

The specimen was not dissected so as not to damage what is probably the largest *Dendrodoris* ever found.

Discussion: Three large *Dendrodoris* with compound pustules on the mantle are known from the Indo-Pacific: *Dendrodoris tuberculosa* (Quoy & Gaimard 1832-33), *D. carbunculosa* (Kelaart 1858) and *D. pustulosa* (Alder & Hancock 1864). The original description of *D. tuberculosa* from New Guinea is brief: it has characteristic tubercles (but in what way they are characteristic is not stated), yellow-brown above, brown below with a series of white circles surrounded by brown rings, and with five gills. The colour plate of this animal is quite different: it appears greyish above with blue-green rhinophores arising from turrets. These turrets are like the mantle tubercles and are most unusual with three to five rings stacked on top of one another, some having lateral papillae. The foot is cream and the mantle ventrally is green with black-ringed white spots. The oral tentacles are digitiform exactly like those in species of Dorididae and unlike a dendrodorid.

Kelaart's *D. carbunculosa* was about 11 cm long (nearly 4½ inches), pinkish-purple, with large warty nodules of which the largest arise from tubercular ringed bases, with five gills and the underside pink (but with no mention of white circles).

Alder & Hancock (1864) certainly thought that they had found Quoy & Gaimard's species, but their drawing of *D. tuberculosa* shows more realistic tubercles and dendrodorid oral tentacle ridges. They also reported white spots ventrally on the mantle, and considered that Kelaart's *carbunculosa* was a probable synonym. They described a smaller animal as a new species, *D. pustulosa*, but this specimen is missing and its underside has not been described. They thought it might be a juvenile of *tuberculosa*.

The collection in the Natural History Museum, London, has more than a dozen specimens of warty *Dendrodoris* between 50 and 80 mm in length, mostly from the Seychelles and other Indian Ocean localities, in the Winckworth collection. They are variously labelled *Dendrodoris tuberculosa*, *D. pustulosa* and *D. carbunculosa*, with most of those possessing white spots being named *tuberculosa*. Most of the specimens have no spaces between the compound tubercles, but some have bare mantle between them.

We have compared our specimen with illustrations labelled *Dendrodoris tuberculosa* by Bertsch & Johnson (1981) from Hawaii and by Wells & Bryce (1993) from Western Australia. The Hawaiian animals have no spaces between the tubercles, while the Australian animal has extensive bare patches on the mantle similar to our specimen. The maximum size given for both Hawaiian and Western Australian animals is 150 mm live (Kay & Young 1969, Wells & Bryce 1993), whereas our specimen is 220 mm preserved.

The main problem with identifying our specimen with Quoy & Gaimard's type material of *D. tuberculosa* is the curious rhinophore turrets, mantle tubercles and oral tentacles shown in their illustration. However, it seems likely that the illustration was prepared by an artist quite unfamiliar with the living animal. If he had already drawn several typical dorids then he may simply have added in the oral tentacles without confirming their actual presence, and the turrets and tubercles may have been artist's licence based on what he thought they must have looked like in life together with the scientists' notes. Moreover, had their animal

been a genuine doridid then it is probable that such a large animal with such peculiar compound tubercles would have been found again and described in the past 170 years. The important question is how many large warty *Dendrodoris* are there in the Indo-Pacific? If there is just one species in which white rings on the mantle may be present or absent, and in which tubercles may be close together or spaced, then our specimen is clearly *Dendrodoris tuberculosa* Quoy & Gaimard, 1832, with *D. carbunculosa* Kelaart, 1858, and *D. pustulosa* Alder & Hancock, 1864, as junior synonyms. But if there is more than one species, and if presence or absence of white circles on the mantle is a diagnostic character, then our animal cannot be *tuberculosa*. The underside of the mantle of the next available name (*carbunculosa*) was unfortunately not described, but the white spots are such a conspicuous feature of *tuberculosa* that it is probable that Kelaart (1858, 1859) would have described them had they been present in his material. *D. carbunculosa* could therefore be used for the taxon lacking white spots. The third species, *D. pustulosa*, is based on a juvenile of either *tuberculosa* or *carbunculosa* and the specimen is missing. If there is just one species of tubercular *Dendrodoris* then this is clearly a junior synonym, but if there are two species then *pustulosa* is likely to remain *incertae sedis*. Pending a thorough revision of these large tubercular *Dendrodoris*, we conclude that there is at present no overwhelming evidence for their being more than one species in the Indo-Pacific, and we therefore identify our specimen as *Dendrodoris tuberculosa* (Quoy & Gaimard, 1832).

Family Phyllidiidae

Phyllidiella annulata (Gray, 1853)

Material: **Henderson Island**, 1 specimen at 28.5 m depth, crawling over sediment on the fore reef slope, 5.12.91.

Description: The living animal is black with raised, flat-topped pink tubercles on the mantle, and paler pink spots near the mantle edge. The largest tubercles each have a central black spot. The rhinophores are black. Preserved in alcohol, the specimen is 16 mm long, the pattern of pale spots and tubercles is retained, but the pink pigment has dissolved away leaving white tubercles. The entire ventral surface is grey, with the edge of the foot white and the sides of the foot darker grey. The colour pattern agrees closely with that illustrated and described by Brunckhorst (1993: Plate 5, G, H).

This species occurs widely in the Indian and Pacific Oceans with records from the Red Sea, Reunion, Indonesia, Guam and Fiji (Brunckhorst 1993).

Phyllidiella pustulosa (Cuvier, 1804)

Material: **Oeno Atoll**, 4 specimens under a stone from 1 m depth, 6.11.91.

Description and discussion: Field notes describe the living animals as "black with pink tubercles on the dorsum". The preserved specimens are 11, 20, 21 and 25 mm long. The mantle is black with numerous low raised white tubercles. The central ones are compound, irregular in shape with two or three peaks. The edge of the mantle is pale although this band is very narrow and broken in some specimens. The rhinophores are black with at least 16 perfoliations. Ventrally the foot, mantle, gills and oral tentacles are grey with the edge of the foot white.

This species varies considerably in the size and density of the raised tubercles such that it has been described under many different names: Brunckhorst (1993) gives a detailed synonymy. Our specimens are almost identical with Brunckhorst's Plate 5 F, and can be confidently assigned to *Ph. pustulosa* on the basis of their pattern of tubercles which is quite different from that of other species in the genus. *Ph. pustulosa* occurs widely in the Indian Ocean from the Red Sea to the Maldive Islands, Thailand and Western Australia, and in the Pacific Ocean from Japan, Queensland and New South Wales eastwards to Guam, Fiji and Tonga (Brunckhorst 1993). Paulay (1989) recorded a specimen from Oeno Atoll as "*Phyllidia*

sp. ? *pustulosa* Cuvier, 1804". It is possible that this is a different species of *Phyllidiella*, such as *Ph. annulata*, because until Brunckhorst's 1993 paper there has been much confusion in identification of phyllidiids. However, since we have found *Ph. pustulosa* on precisely the same atoll, we are confident that Paulay's specimen belongs to this common and widely distributed species.

Suborder Dendronotacea

Family Bornellidae

***Bornella irvingi* n. sp.**

(Figs 5, 6)

Bornella n. sp. Preece, 1995; p. 358.

Material: **Ducie Atoll**, 2 specimens at 12–15 m depth under a coral, 24.10.1991 (UMZC reg. no. I 22000a (holotype) and I 22000b (paratype)).

Description: Colour photographs show that in life the larger animal has the body white with the head black, and the edge of the foot orange with a black band just inside the orange (Fig. 5A, B). Orange viscera are visible through the lateral body wall. The dorsal papillae and gills are white. The rhinophore sheath is black, the long dorsal papilla has a white base and is orange distally while the three distal sheath papillae are orange. The rhinophore club is just visible in one of the colour pictures and is white. The oral papillae are orange. The smaller animal has similar colour markings but lacks black pigment; instead the head and

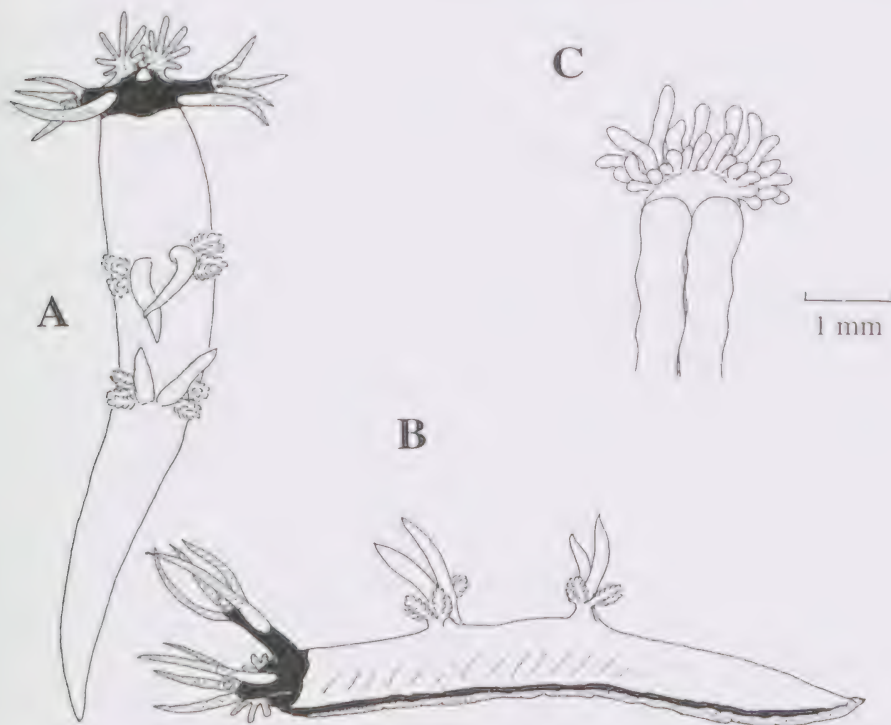


Fig. 5. *Bornella irvingi* n. sp., holotype. A. Dorsal view of living animal from a colour slide. B. Lateral view of living animal from a colour slide. C. Ventral view of head of preserved animal. Stipple is orange.

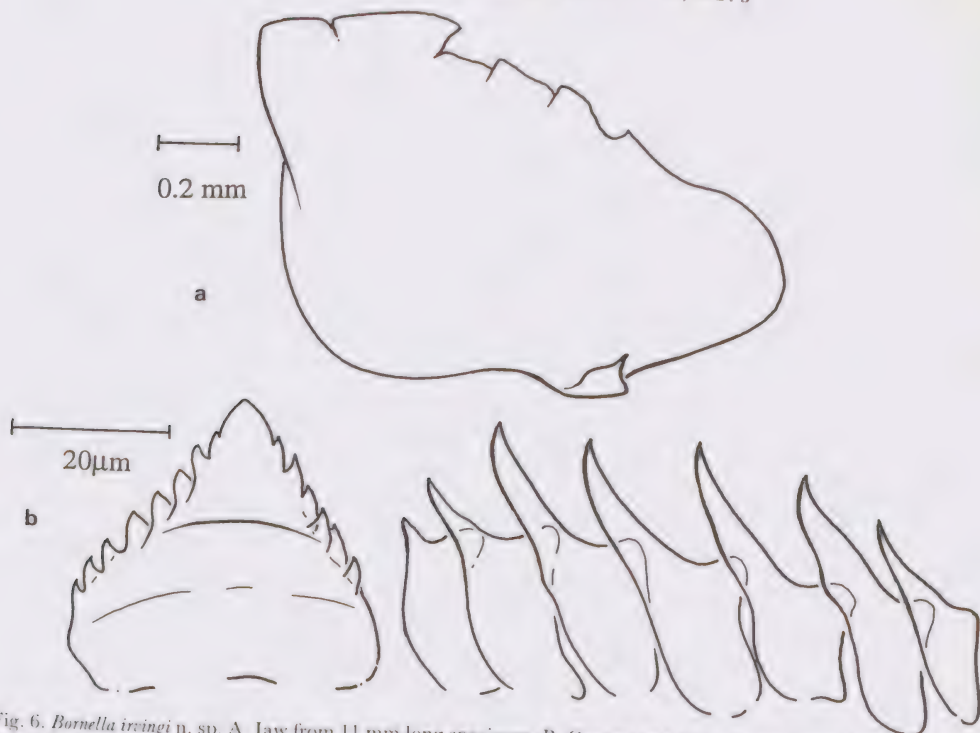


Fig. 6. *Bornella irvingi* n. sp. A. Jaw from 11 mm long specimen. B. Central and seven lateral teeth from 45th row of the radula of 11 mm long specimen.

rhinophore sheaths are white and the foot edge is orange with a slightly darker orange just inside the edge.

The two specimens are 16 and 11 mm long preserved and all pigment has dissolved out in the preservative. The body is much flattened laterally. There are two pairs of lanceolate papillae arising close to the dorsal midline. Each papilla has two gills at its base on the outer side, each with more than one branch and irregularly 1- or 2- pinnate. The rhinophores are club. Each rhinophoral sheath ends in three papillae and has one longer papilla arising dorsolaterally near its base, but the smaller animal has the right sheath ending in just two papillae. There are thirteen oral papillae dorsally on each side of the mouth (Fig. 5C). The foot is folded longitudinally and notched anteriorly.

The buccal mass from the smaller animal was examined. The jaws are 1.25 mm long, oval in shape (Fig. 6A). The radular formula is $46 \times 7.1.7$. The radular ribbon is sharply angled with 14 rows in the younger part (plus one in process of formation), and 32 in the older. The median tooth is broad and pointed with six or seven denticles on each side, the medial ones arising from the main cusp (Fig. 6B). The six or seven lateral teeth each have a lanceolate, pointed cusp arising from a rectangular plate (Fig. 6B).

Derivatio nominis: This species is named after Robert Irving, one of the divers, who collected these specimens.

Discussion: Bertsch (1980) gives a list of the currently recognised species of *Bornella* Gray,

1850, and three additional species have been described since then. *B. irvingi* can be distinguished from these species as follows:-

B. stellifer (Adams & Reeve in Adams, 1848) is type of the genus with nine synonyms and a wide distribution in the Indian and Pacific Oceans (Bertsch 1980, Rudman 1984). It differs in colour and in having many more bunches of cerata.

B. calcarata Mörch, 1863 from the Caribbean is the only Atlantic species, and differs in colour and numbers of cerata.

B. japonica Baba, 1949 from Japan also differs in colour and numbers of cerata.

B. excepta Bergh, 1884 from the East Indies and Zanzibar (Eliot 1904) differs in colour and in having more processes on the rhinophore sheath.

B. simplex Eliot, 1904 from Zanzibar differs in colour and in having fewer oral processes.

B. sarape Bertsch, 1980 from the Gulf of California differs in colour, in having more papillae per bunch of cerata and more processes on the rhinophore sheath.

B. anguilla Johnson, 1983 from Hawaii, Western Australia, Mauritius and South Africa (Gosliner 1987, Yonow & Hayward 1991, Wells & Bryce 1993) is unusual in its striking colour pattern of orange-red and black and in having flattened cerata and rhinophoral processes.

B. irvingi differs from all known species of *Bornella* in its orange, white and black colour pattern and in the small number of ceratal papillae. Too few collections of nudibranchs have been made in the Pacific to know whether this species has a wide geographical range or if it is restricted to one or a few islands in the Pitcairn group.

DISCUSSION

The composition and relationship of the marine molluscan fauna from these remote islands has recently been reviewed by Preece (1995). Three previous records of opisthobranchs collected from the Pitcairn group of islands in 1987 by Paulay have been given already in the systematic section. Two additional records follow:

Rehder & Randall (1975) recorded *Dolabrifera* cf. *fusca* Pease, 1868, from the gut of a *Coris aygula* speared off the northwest corner of Ducie Atoll. This is probably a synonym of the common pan-tropical *Dolabrifera dolabrifera* (Cuvier, 1817).

Glaucus atlanticus Forster, 1777 was found in 1987 on Henderson by Paulay (1989).

This collection of opisthobranchs comprises twenty species, which must be a very small proportion of the opisthobranchs that actually occur in these islands. Recent publications suggest that there are several hundred species of opisthobranchs in the Indo-Pacific: Rudman (1990, and references therein) has recorded more than 120 species of a single family, the Chromodorididae, which is currently unrecorded from the Pitcairn area. The majority of Indo-Pacific opisthobranchs occur in shallow waters with coral reefs of high biodiversity. The seas, coasts and atolls around south-east Asia and northern Australia are the centre of this region and probably have the largest numbers of species, and we can expect numbers to fall off as one travels east in the Pacific because there are much larger areas of deep sea unsuited to shallow-water reef species. Nevertheless Bertsch & Johnson (1981) report 77 species of opisthobranch from the Hawaiian Islands, and many more have been recorded but not included in this popular guide. Similar numbers probably occur further south in Polynesia, but these areas have been much less well studied. The small number of species recorded undoubtedly reflects collecting deficiencies, but large to medium-sized nudibranchs did appear to be genuinely less common than on reefs studied elsewhere (R. Irving, pers. comm.). We can therefore expect many more species to be found in this area, including more endemics like *Bornella irvingi*, currently known only from the somewhat isolated Ducie Atoll.

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A NEW GENUS OF ATLANTIC MURICIDAE WITH MISLEADING SHELL MORPHOLOGY (MOLLUSCA: GASTROPODA)

PHILIPPE BOUCHET¹ AND ROLAND HOUART²

Abstract: Abstract: The tropical West African *Murex gubbi* Reeve, 1849, until now classified in *Chicoreus* (subfamily Muricinae), is made the type of the new genus *Chicocenebra* (subfamily Ocenebrinae), based on radular and shell morphology. The species had been erroneously classified due to the convergence of its shell with species in the wrong subfamily.

Key words: Muricidae, New Genus, West Africa

INTRODUCTION

Whereas most species of Muricidae can be unequivocally assigned to family and even often to subfamily based on shell characters, a few others are convergent with several neogastropod families. Such muricids were originally described in the "wrong" family, or conversely species described as Muricidae belong in fact to other families. Within Muricidae, shell convergence occurs also among the different subfamilies of this large family.

In this paper, as a result of routine taxonomical work on tropical Atlantic gastropods, we report on a new case of conchological convergence among the subfamilies Muricinae and Ocenebrinae. Convergence of shell characters is revealed by examination of the radula, and necessitates the erection of a new genus.

SYSTEMATIC DESCRIPTION

Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossmann, 1903

Chicocenebra n. gen.

Type species: *Murex gubbi* Reeve, 1849.

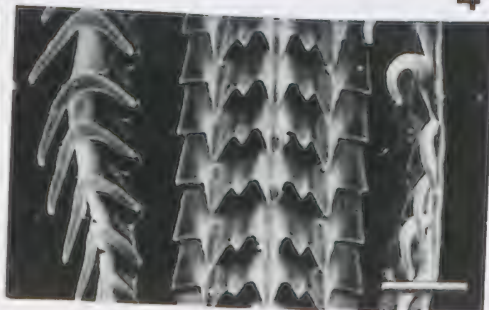
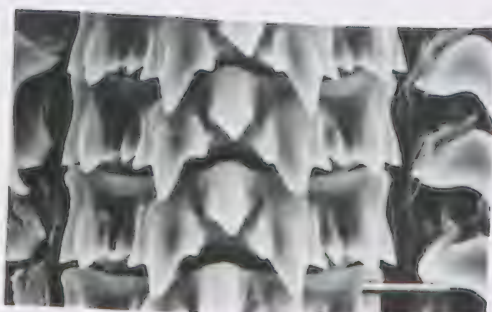
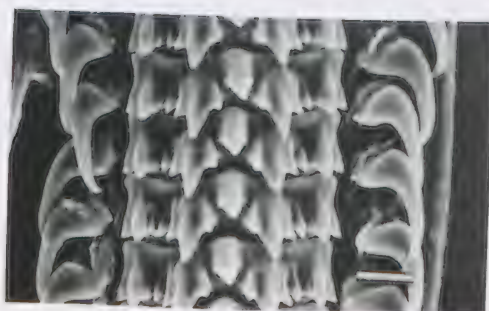
West Africa, from Gabon to northern Angola, subtidally to 50 m.

Description: Muricid with typical ocenebrine radula (Figs. 3-4): rachidian tooth with short projecting central cusp, long lateral cusp with inner lateral denticle on base, marginal area with several denticles, marginal cusp large.

Shell large, solid, several centimetres high. Spire high, with trivariolate whorls (except the first and second teleoconch whorls which have low, rounded axial ribs). Spiral sculpture consisting of nodulose cords of various strength. Aperture ovate, relatively narrow, outer lip

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strongly denticulate within, with a deep adapical sinus continuing into the open, long, frondose shoulder spine. Siphonal canal open, relatively short (ca. 25% of total shell height).

Operculum ovate, lateral nucleus in lower right (Fig. 2).

Etymology: A combination of *Chicoreus*, a trivariate muricine genus, and *Ocenebra*, the type genus of Ocenebrinae.

Remarks: Based on shell characters, *Murex gubbi* is usually treated in the recent literature (e.g., Vokes 1971, Fair 1976, Radwin & D'Attilio 1976, Bernard 1984, Gofas *et al.* 1985) as a species of *Chicoreus* Montfort, 1810, hence a member of the subfamily Muricinae. The general shell outline is especially convergent with *Chicoreus (Triplex)*, but *C. gubbi* differs in its strongly denticulate aperture, channeled shoulder spine, and relatively short siphonal canal. Furthermore, the rachidian tooth of the radula unequivocally places *Chicocenebra* in the subfamily Ocenebrinae (Figs. 3–5), rather than in Muricinae (Fig. 6).

From *Ocenebra* (type species: *Murex erinaceus* Linné, 1758), *Chicocenebra* differs in its consistently trivariate shell, open siphonal canal, strongly denticulate aperture, and channeled shoulder spine. In *Ocenebra isaaci* Houart, 1984, a somewhat atypical member of *Ocenebra*, only the penultimate and body whorls are trivariate, and the aperture is weakly denticulate without a channeled shoulder spine.

Chicocenebra differs from the other trivariate ocenebrine taxa [*Jaton* Pusch, 1837, *Ceratostoma* Hermannsen, 1846, *Poropteron* Jousseaume, 1880, *Pteropurpura* Jousseaume, 1880, *Calciatrapessa* Berry, 1959 and *Microrhytis* Emerson, 1959] in the peculiar denticulate aperture, the channeled shoulder spine, the open siphonal canal and the numerous, frondose varical spines. From *Ceratostoma* and *Microrhytis*, it differs also by the absence of a labral tooth.

DISCUSSION

Shell convergence among the subfamilies of Muricidae has also been reported before on several occasions. For instance, the genus *Nucella* Röding, 1798 has commonly been classified in Thaidinae (now Rapaninae), however Kool (1993) suggested a position in Ocenebrinae, based on anatomy, radula, protoconch, shell ultrastructure and operculum characters. The genus *Spinidrupa* Habe & Kosuge, 1966 was transferred from the Rapaninae to the Ergalataxinae based on shell and radular morphology (Houart 1995a). Another species, *Murex (Ocinebra?) painei* Dall, 1903, was long considered as an ocenebrine. However, recent studies based on shell and radular characters reassigned it to the Trophoninae (D'Attilio 1980, McLean 1995). Small species of muricids from New Caledonia have been described as Muricinae in the subgenus *Poirieria* (*Paziella*) based on shell characters (Houart 1986) and then reallocated to Trophoninae based on radular morphology (Houart 1995b).

Despite these numerous examples, once knowledge of radula and other discriminant characters has been acquired, shell convergence among muricid subfamilies may be judged to be rather superficial. Indeed, allocation of muricid taxa to the appropriate subfamily is often possible from careful appraisal of shell morphology alone. This is most important for paleontologists, who must base their suprageneric groupings of fossil muricid clades on shell characters alone.

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Figs. 1–6. *Chicocenebra gubbi* (1–4) and other muricid radulae for comparison (5–6). 1, *Chicocenebra gubbi* (Reeve, 1849), Gabon, 49.1 mm, coll. R. Houart. 2, Operculum of a specimen from Angola, scale bar 3 mm. 3–4, Radula of a specimen from Angola, scale bar 20 μ m. 5, Radula of *Ocenebra erinaceus* (Linné, 1758), specimen from Brittany, France, scale bar 50 μ m. 6, Radula of *Chicoreus (Triplex) paini* Houart, 1983, specimen from the Solomon Islands, scale bar 50 μ m.

With *Murex gubbi* now reallocated to a new genus of Ocenebrinae, *Chicoreus* is left without any Eastern Atlantic representative.

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SMALL NUCULIDAE (BIVALVIA) WITH FUNCTIONAL PRIMARY HINGE IN THE ADULTS

SERGE GOFAS¹ AND CARMEN SALAS²

Abstract: Two pedomorphic species of the family Nuculidae are described from the Western Mediterranean and the Canary Islands respectively. They have an adult size close to 1 mm and maintain a functional set of 9-12 primary teeth, jointly with a small number of the usual taxodont teeth of the nuculids. The larger species *Nucula nucleus* and others have lost such teeth at the same size.

The two new species have a smooth ventral margin, a character shared with juveniles of all species with a crenulated margin in adult stage. The value of this character at the generic level is discussed; the new species are found to share more characters with *Nucula* s. str. than with larger species with a smooth margin in the adult stage currently classified as *Ennucula*, and thus are provisionally retained in the genus *Nucula*.

Key words: Taxonomy, Nuculidae, Mediterranean, Canary Islands, pedomorphosis.

INTRODUCTION

The family Nuculidae is represented in Eastern Atlantic and Mediterranean Sea by about 10 species, each one with a specific bathymetrical range on the continental shelf or slope. All of them are centimetric in size at the adult stage. Nuculid species with a very small adult size are known in the Atlantic only from the Caribbean (Moore, 1977).

Two species from European seas, reaching little more than 1 mm in adult size, are described here. Attention was first drawn by a very small Canarian species, which is the only littoral representative of the family in the Archipelago. A similar species was later found in the Mediterranean, and obviously had been mistaken for juveniles of the larger species. Both are characterised by having a functional set of primary teeth (terminology of Bergmans, 1978).

For comparison, growth series of all the European littoral and some deeper water species were observed in selected populations where identification is not problematic.

MATERIAL

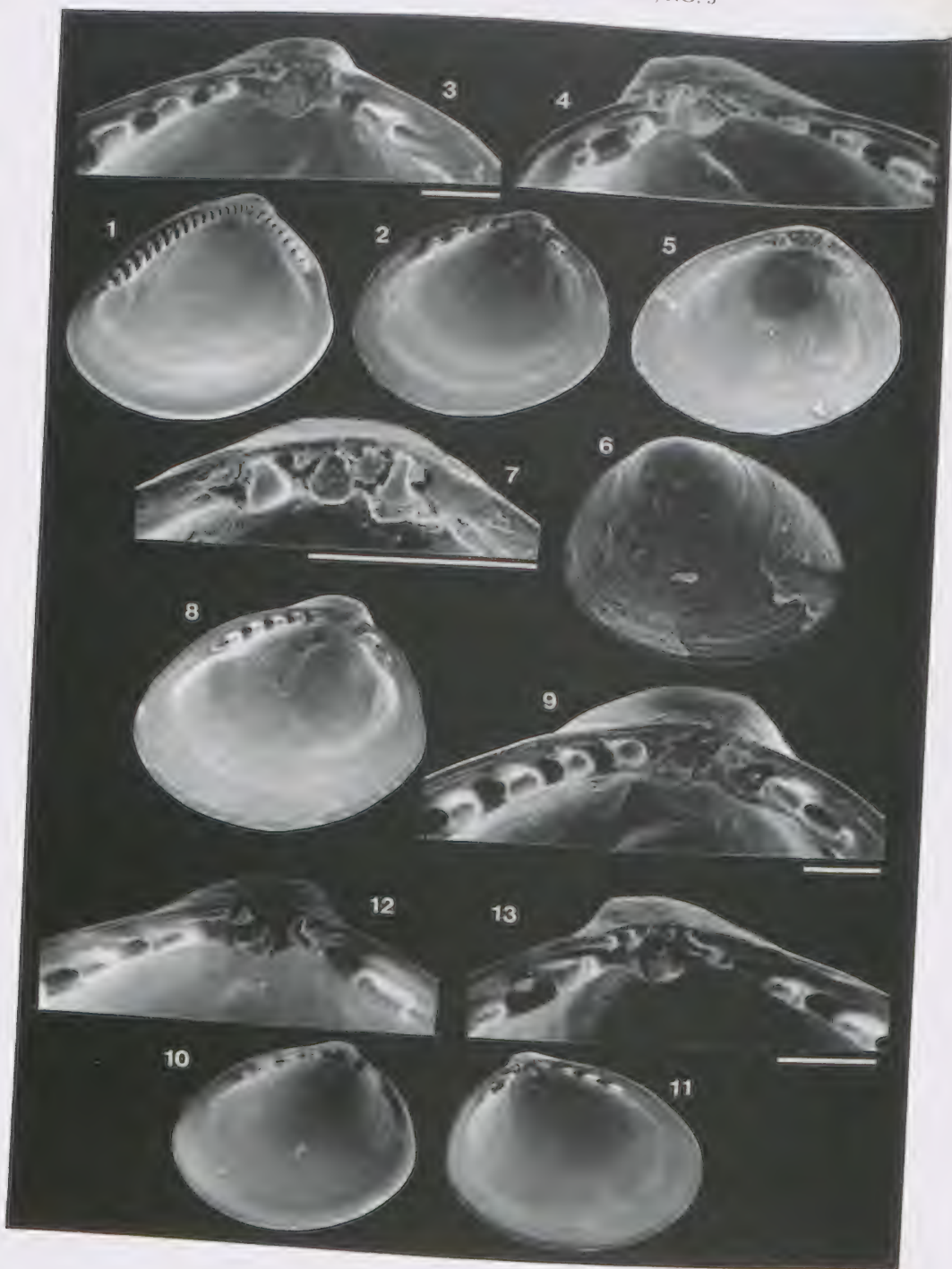
The material for this study was primarily derived from the following excursions:

– intertidal collecting in the Canary Islands by P. Bouchet (MNHN) in 1981, housed in Muséum National d'Histoire Naturelle, Paris (MNHN).

– FAUNA I expedition of R/V "Garcia del Cid" dedicated to sampling the shelf fauna of the Southern Iberian Peninsula, as a part of the FAUNA project of the Spanish Research Council DGCYT. Material in Museo Nacional de Ciencias Naturales, Madrid (MNCN).

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- monthly survey of a *Posidonia* bed in the Cabo de Gata-Níjar national park (Almería, Spain). Material in Universidad de Málaga.
- dredging around Roscoff (Finistère, France) in June 1994, particularly targeted to collecting juvenile *Nucula*. Material in MNHN.

The BALGIM expedition (MNHN) sampled the shelf and slope faunas at the Mediterranean/Atlantic transition, and yielded material of most European nukulids. This has provided adequate material for comparisons, which is listed and figured elsewhere (Salas, 1996).

SYSTEMATICS

Nucula nucleus (Linné, 1758)

Material examined: Roscoff, "les Cochons Noirs" (40°43.0'N, 3°51.8'W), 20 m on bioclastic coarse sand: ca. 50 specs (0.4 × 0.35 to 10.0 × 9.5 mm), leg. Gofas 6/1994.

Description: The protoconch of *N. nucleus* is rounded, ca. 180 µm in diameter, with an apical depression separating two indistinct bumps; its surface is irregularly covered with minute punctures. The earliest part of the teleoconch has an external microsculpture of radial threads, starting at the very edge of the protoconch and then gradually fading.

Specimens less than 0.5 mm have only the primary teeth developed (figure 5); these are few in number (2 in the figured specimen) and are fully functional at this stage; the ligament is almost vertical and deeply wedged between them. Secondary teeth begin forming when shell size reaches 0.5 mm, starting with the anterior part of the hinge, and increase in number gradually with size, as more teeth are added at the distal end of each series.

At a shell length of ca. 1 mm, there are 1–2 secondary teeth on the posterior part of the hinge and 3–4 on the anterior part (fig. 2–4). The ligament points slightly obliquely forwards and is deeply wedged between the two segments of teeth; the primary teeth may still be seen above it (fig. 3–4) but are set apart from the lower hinge margin at this stage. The ventral margin of the shell is smooth.

The crenulations on the ventral margin appear quite suddenly at a size of 1.1 to 1.2 mm, the number of crenulations being ca. 55, increasing to ca. 70–75 in adults of 7 mm length. The number of secondary teeth also gradually increases, reaching 3–4 posterior and 8–9 anterior at a size of 2 mm, and 11–12 anterior and 22–24 posterior at final size; the adapical teeth of the anterior segment narrow very much and overrun the ligament, which becomes very oblique (fig. 1).

Nucula hanleyi Winckworth, 1930

Material examined: Roscoff, "les Cochons Noirs", 20 m on bioclastic coarse sand: ca. 200 specimens (0.5 × 0.4 to 12.0 × 9.5 mm), leg. Gofas 6/1994. Bay of Algeciras, 3 specs (1.1 × 0.9 to 1.7 × 1.4 mm). Almeria, Playa de los Genoveses, (0.8 × 0.65 to 1.8 × 1.5 mm), 5 specs. (5 m, 2/1987), 3 specs (5 m, 4/1987), 4 specs (7 m, 10/1987).

Description: Specimens as small as 0.5 mm of *N. hanleyi* are easily separated from the sympatric *N. nucleus* by their more elongate contour. Larger specimens of *N. hanleyi* also differ by having radial rays on the periostracum, and (Warén, pers. comm.) by having 3 loops in

Figs. 1–13. *Nucula nucleus* (Linné, 1758), Roscoff. 1: right valve of adult (7.1 mm). 2: right valve of juvenile (1.0 mm). 3–4: hinges of right and left valves of specimen fig. 2. 5–6: right valve of juvenile (0.4 mm). 7: Hinge of the valve fig. 5 (scale bar 100 µm). *Nucula nitidosa* Winckworth, 1930, Roscoff. 8: right valve of juvenile (1.1 mm). 9: Hinge of the same valve (scale bar 100 µm). *Nucula hanleyi* Winckworth, 1930, Playa de los Genoveses. 10–11: right and left valve of juvenile (1.1 mm). 12–13: Hinge of the same specimen (scale bar 100 µm).

the intestine instead of 4. In Roscoff, the separation of the two species in a microsympatric population is clearcut, with no ambiguous individuals; the same does not hold for the Southern Iberian populations, where it is not possible to discriminate convincingly two species, and where all specimens may belong to *N. hanleyi* notwithstanding the occurrence of specimens which mimic the northern *N. nucleus*.

There is no essential difference in the ontogenetic sequence, compared to *N. nucleus*. The crenulations also appear quite suddenly between 1.1 and 1.2 mm of shell length, but correlatively with the longer ventral margin, may rise to number 90–100 in a 10 mm adult.

***Nucula nitidosa* Winckworth, 1930**

Material examined: Roscoff, "Pierre Noire" (48°42.6'N, 3°51.8'W), ca. 100 specs. (1.1 × 0.95 to 9.8 × 8 mm). Picard leg., 1964; Spain. Redondela, FAUNA 1 – 71A, 37°09.48'N, 07°13.56'W, 13–15 m, muddy sand, 23.7.1989: 645 specs. (0.85 × 0.7 to 6.5 × 5 mm).

Description: The protoconch of *N. nitidosa* is rounded, ca. 150 μ m in diameter, with a very shallow apical depression; its surface is quite smooth with some areas with minute punctures; it is usually decorticated even on specimens less than 1 mm, probably due to corrosive interstitial water in the preferred sediment. The earliest part of the teleoconch has a very dense but tenuous external microsculpture of radial threads, starting at the very edge of the protoconch and quickly fading. There is a characteristic swelling of the early part of the teleoconch which is not found in *N. nucleus* or *N. hanleyi* (compare fig. 9 with fig. 3 or 12).

At a shell length of ca. 1 mm, there are 1–2 secondary teeth on the posterior part of the hinge and 4–5 on the anterior part (fig. 8). The ligament points slightly obliquely forwards and is deeply wedged between the two segments of teeth; the primary teeth have virtually disappeared at this stage. The ventral margin of the shell is smooth.

The crenulations on the ventral margin appear quite suddenly at a size of 1.1 to 1.2 mm. In this species, the onset of the radial rods underlying the crenulations is conspicuous in transmitting light; in a valve 1.2 × 1 mm, the radial structure starts at ca. 0.3 mm from the ventral margin and is clearly defined in separate rods at 0.1 mm from the margin.

Very small *N. nitidosa* already have a distinctive glossy periostracum, and some fine concentric ridges towards the anterior end. Although all three species are broadly sympatric, *N. nitidosa* prefers more muddy substrates and does not occur together with *N. nucleus* and *N. hanleyi*.

***Nucula recondita* n. sp. (figures 14–22)**

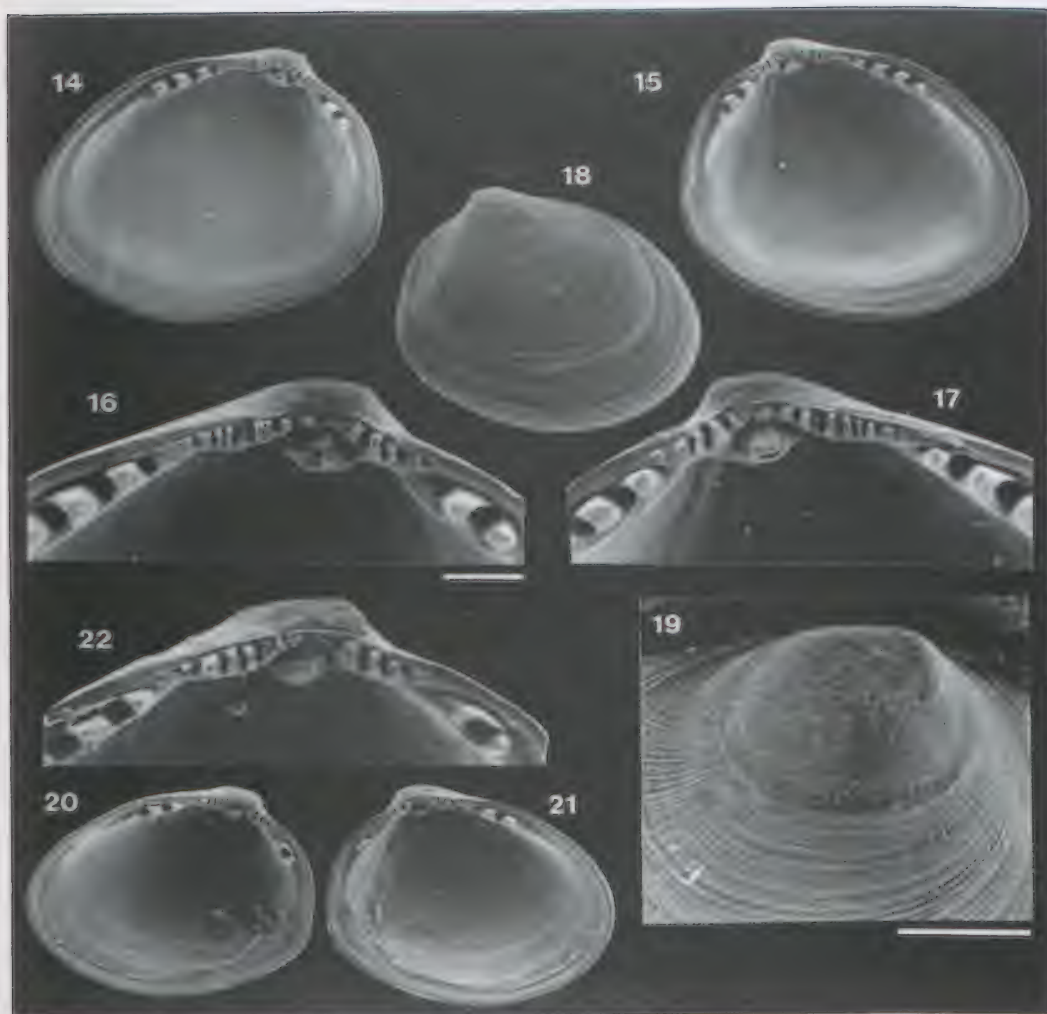
Type material: Holotype (MNCN) and 6 paratypes (3 dry: MNHN, 3 wet: MNCN) from the type locality, Fauna 1: 33A, 15.7.1989.

Type locality: Alboran Island, 35°56'N – 03°02'W, 34–44 m, rocky bottom with *Laminaria*.

Material examined: The type material (1.0 × 0.85 to 1.1 × 0.95 mm); Almeria, Playa de los Genoveses, 4.5–6 m in Posidonia beds, 23 specs., Hergueta leg. 1987 (0.65 × 0.4 to 1.1 × 0.85 mm; University of Málaga). Calahonda, beach drift, 1 shell (0.90 × 0.70 mm; MNHN). Fréjus, Le Dramout (43°24.7'N–6°5.17'E), 22–30 m, 9 shells and 7 valves, Pelorce leg. 1992 (MNHN).

Description: Shell minute, up to 1.1 mm length (holotype 1.0 × 0.85 mm), moderately solid, equivalve and rather inflated, inequilateral, subtrapezoidal-ovate in outline; beaks behind the vertical midline. Anterior dorsal margin curved; at first gently, then abruptly sloping downwards to the rounded anterior margin. Posterior margin convex; at first sloping downwards from the beak, then abruptly truncated. Ventral margin broadly rounded. Periostracum light greenish brown.

Protoconch rounded, about 200 μ m in diameter, with an apical depression. Surface rugose and pitted, except on the edge which is nearly smooth. Teleoconch with both radial and concentric microsculpture. Radial threads thin and narrower than the interspaces.



Figs. 14–22. *Nucula recondita* n. sp., Alboran Island (Fauna 1, 33A). 14–15: right and left valves of a paratype, inner views (1.1 mm). 16–17: Hinge of the same specimen (scale bar 100 μ m). 18: Holotype, external view of the right valve (1.0 mm). 19: Protoconch of another paratype (scale bar 100 μ m). *Nucula recondita* n. sp., Playa de los Genoveses. 20–21: right and left valve, inner views (0.9 mm). 22: Hinge of the right valve (scale bar 100 μ m).

slightly divergent towards the anterior and posterior ends. Concentric threads, very thin and narrower than the interspaces on the early part of the teleconch and later hardly distinct from the growth lines.

Hinge with the anterior part slightly longer than the posterior, with both primary and secondary teeth. Primary teeth narrow, occupying about half of the hinge plate, 8–10 anterior to the chondrophore and 5 posterior to it. Secondary teeth broad, knob-like, 3–4 anterior and 2–3 posterior on each valve. Chondrophore broad, more or less symmetrical, adjacent to a narrowing portion of the hinge plate, with a rounded lower margin.

Inside of valves with two ill-defined ovate adductor muscle scars. Pallial line entire, ill-defined. Smooth ventral margin.

Etymology: *reconditus*, Latin meaning hidden.

Habitat: Among algae on infralittoral hard bottoms, subtidal between 5 and 40 m.

Distribution: Presently known from the Alboran Sea and the French Mediterranean coast. *Remarks*: This species externally resembles the juveniles of the other littoral nuculids, particularly *N. hanleyi*, with which it has been found sympatrically. It differs essentially by the presence of well developed and functional primary teeth occupying about half of the hinge. Such teeth are inconspicuous in the other species at similar sizes. Also, the radial threads on the early part of the teleoconch are never so dense in any of the larger European nuculids. In addition to these definitive characters, the trapezoidal outline and more prominent beaks usually allow the recognition of this species prior to opening the hinge.

The most closely related species is *N. bicornis* n. sp., which shares the presence of primary teeth in the hinge and the external teleoconch sculpture. It is readily distinguished by the protoconch and the outline.

Nucula bicornis n. sp. (figures 23–27)

Type material: Holotype (MNHN) and 15 paratypes (5 MNHN, 5 MNCN, 5 Museo Insular de Ciencias naturales, Tenerife) from the type locality, Bouchet leg. 7/1981.

Type locality: Palm-mar, Tenerife, 28°02'N, 16°42'W, intertidal in algal mat on rocks.

Material examined: Tenerife (all Bouchet leg. 7/1980; MNHN except specified paratypes) – The type material (0.7 × 0.55 to 0.95 × 0.75 mm); Las Galletas, 9 specs. (0.45 × 0.3 to 0.85 × 0.7 mm); Los Cristianos, 3 sh. (0.55 × 0.4 to 0.65 × 0.5 mm); Punta de Teno, 2 specs. (0.6 × 0.45 mm). Lanzarote – La Isleta, 1 spec. (0.75 × 0.6 mm), Bouchet leg. 12/1981. Selvagens Islands – Selvagem Grande, 2 specs. (0.5 × 0.4 to 0.8 × 0.65 mm), Segonzac leg. 7/1989 (MNHN).

Description: Shell minute, up to 0.95 mm length (holotype 0.90 × 0.75 mm), moderately solid, equi-convex and rather compressed, inequilateral, subtriangular-ovate in outline; beaks salient, behind the vertical midline. Anterior dorsal margin curved, at first nearly horizontal, then abruptly sloping downwards to the rounded anterior margin. Posterior margin slightly to strongly convex. Ventral margin broadly rounded. Periostracum light greenish brown.

Protoconch rounded, about 160 µm in diameter, with two strong ridges delimiting an apical depression. Surface rugose and pitted, except on the edges where it is nearly smooth. Teleoconch with both radial and concentric microsculpture. Radial threads thin and narrower than the interspaces, stronger and slightly divergent towards the anterior and posterior ends. Concentric threads very thin and narrower than the interspaces on the early part of the teleoconch, then gradually merging with the growth lines towards the ventral margin.

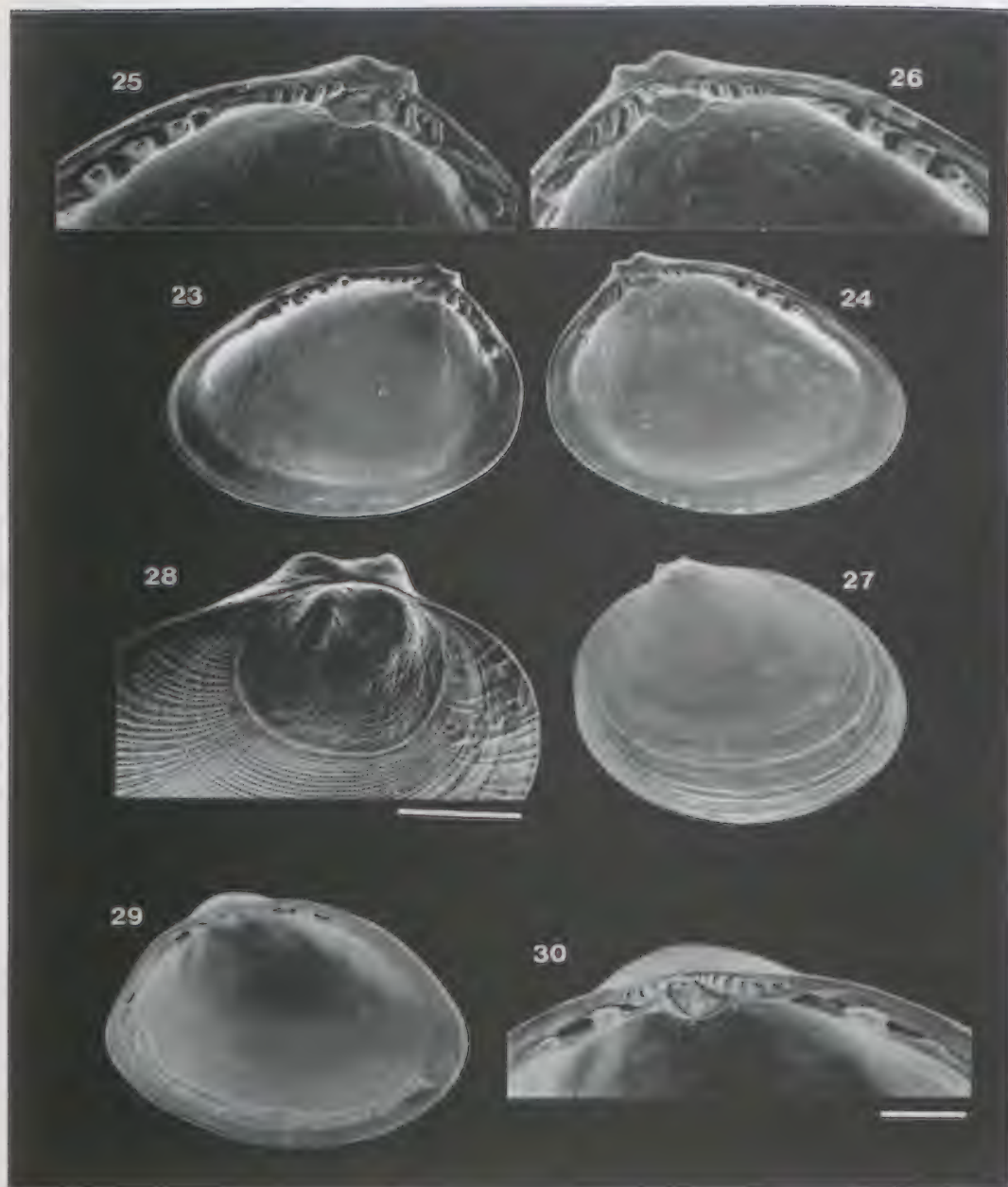
Hinge narrow, anterior part about twice as long as the posterior, with both primary and secondary teeth. Primary teeth narrow, occupying about half of the hinge plate, 4–5 anterior to the chondrophore and 3–4 posterior to it. Secondary teeth broad, knob-like, 4 anterior and only one posterior on each valve. Chondrophore broadly triangular, slightly oblique, deeply wedged into the hinge plate, with a rounded lower margin.

Inside of the valves with two quite conspicuous, rounded adductor muscles scars. Pallial line entire, ill defined. Smooth ventral margin.

Etymology: *bicornis*, Latin meaning double horned and referring to the two ridges on the protoconch.

Habitat: Intertidal rocks in algal mat.

Distribution: Known only from Tenerife, Lanzarote and Selvagens Islands. It is probably present in the other islands of the Canarian Archipelago, but not documented.



Figs. 23–27. *Nucula bicornis* n. sp., Palm-Mar, Tenerife. 23–24: right and left valves of a paratype, inner views (0.95 mm). 25–26: Hinge of the same specimen (scale bar 100 μ m). 27: Holotype, external view of the right valve (0.90 mm). 28: *Nucula bicornis* n. sp., Las Galletas, Tenerife. Protoconch. 29–30. *Ennucula aegeensis* (Forbes, 1844), Alboran Sea, “Balgim” sta. DW 147 (35°50'N 04°58'W), 489 m. 29: left valve of a juvenile (1.0 mm). 30: Hinge of the same valve (scale bar 100 μ m).

Remarks: This species recalls *Condylonucula* Moore, 1977 by the small size and the outline but it is clearly distinct by the protoconch which has two ridges instead of a prominent central knob, by the lack of the conspicuous concentric ridges and by the hinge with well developed primary teeth.

It is closely allied to *N. recondita* n.sp., but differs by the more prominent protoconch, more triangular outline, lesser number of secondary teeth in the hinge and more deeply wedged chondrophore.

The protoconch of many nukulids has a somewhat depressed apical area, but in *N. bicornis* this character is so exaggerated, that it results in the two peculiar ridges, which make it unmistakable.

This is the only littoral nukulid known to date from the Canary Islands.

DISCUSSION

The distinction between nukulids with smooth and with crenulated margin is currently widely accepted, at least at the genus level. Maxwell (1988) introduced a subfamily Nuculomidae for the species with smooth margins. Taylor, Kennedy & Hall (1969) established that the crenulations are related to an underlying microstructure of aragonitic rods in the outer layer of the shell. We have observed that the type species of *Nucula* and all other examined species first have smooth margins and acquire crenulations with the underlying structure at a size of slightly over 1 mm. Following the widely accepted assumption that a state of character which appears later in ontogeny is derived, a species-group with a smooth margin is diagnosed by a symplesiomorphy. Furthermore, the crenulated character state may be lost through paedomorphosis.

Schenck (1939) and Maxwell (1988) consider that the Recent species with a smooth margin should be included in the genus *Ennucula* Iredale, 1931 (type species *Nucula obliqua* Lamarek, 1819, SD Singleton, 1932), rather than in *Nuculoma* Cossmann, 1907 (type species: *Nucula castor* d'Orbigny, 1849, monotypy) as is usual in the European literature. We have examined type specimens of *N. castor* from the Jurassic of France (MNHN) and agree.

A functional primary hinge resembling that of the new species is maintained at a rather late stage, approximately 1 mm in length, in the bathyal species *Ennucula aegeensis* (Forbes, 1844) (figure 29–30). However, the early teleoconch of this species and the related *E. bushae* (Dollfus, 1898) lack any radial microsculpture; the protoconch is regularly dome-shaped without an apical depression; in the adults, the outline is much less inequilateral and the ligament is less oblique and is lodged in a protruding, spoon-like chondrophore.

The radial microsculpture on the early part of the teleoconch is consistently found on all species of *Nucula* examined, even in species such as *N. nitidosa* with a very smooth and glossy outer surface in the adult stage. This, together with the anteriorly truncated outline and the tendency in the protoconch to form two humps are characters which the two new species share with *Nucula* s. str. and not with *Ennucula*, leaving the smooth margin as the main shared character with the latter.

The Australian species *Nucula cova* Bergmans, 1978 also shows a rather conspicuous series of primary teeth but has radial ribs and a crenulated margin. This suggests that the persistence of primary teeth in Nuculidae, adults or juvenile, is a paedomorphic trait occurring haphazard along several lineages and is not a reliable character for assessing relationships. The genus *Rumptonucula* Bergmans, 1978 is stated in the original description as having primary teeth on each side of the ligament, but Bergman's (1978) figures show a very limited extent of these, similar to the 1 mm stage of *N. nucleus* (see fig. 3–4). The most diagnostic character of *Rumptonucula* is actually the deep notch posterior to the ligament, which is not found in any of the species discussed here.

The two new species share with *Condylonucula* a small adult size. However, the latter lacks a paedomorphic hinge and has a very different protoconch and external sculpture, so that the similarity in size is most likely a convergence.

A possible outcome is that a new genus will be needed to accommodate the two new species. However, a more general overview of the family and a subdivision of the species with a smooth margin into monophyletic units, both beyond the scope of this paper, are desirable before a generic name be introduced; a conservative treatment as species of *Nucula* is considered more appropriate at this stage.

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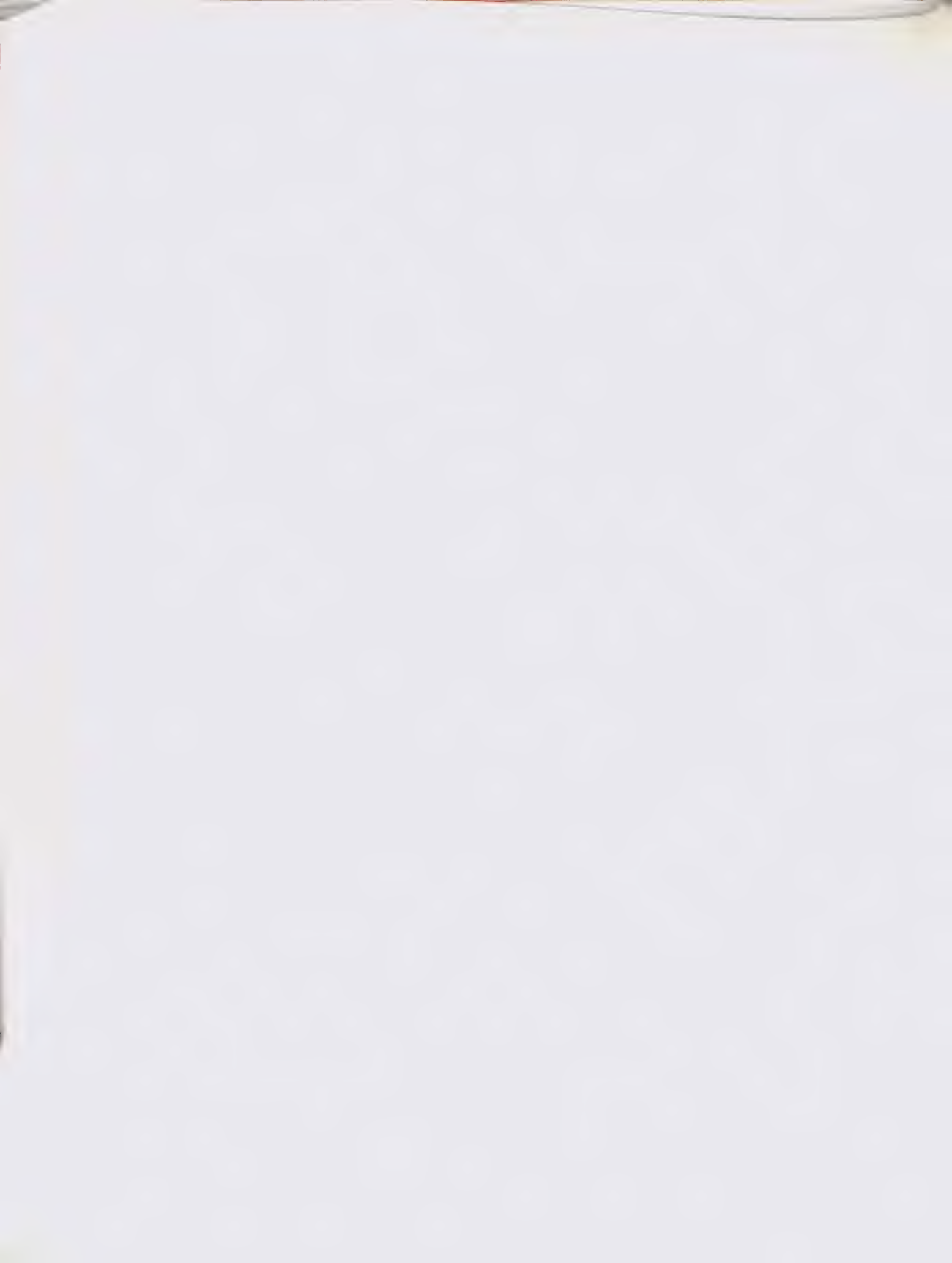
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We are grateful to Franc Gentil for facilities with ship time given in Station Biologique de Roscoff for an essential part of this study; to Hervé Senut (Laboratoire de Paléontologie, MNHN) for the loan of types of *Nucula castor*.

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A SHELL OF *FLORIBELLA ALDRICHI* (DALL, 1890),
A LARGE SEAHARE (MOLLUSCA:
OPISTHOBRANCHIA: APLYSIIDAE) FROM THE
NEOGENE OF THE NORTHERN DOMINICAN
REPUBLIC

D. L. GEIGER¹ AND P. JUNG²

Abstract: A single specimen of the aplysiid *Floribella aldrichi* from the late early to early middle Miocene Baitoa Formation of the Dominican Republic is discussed. So far this rare species is exclusively known from the early Miocene of Florida, the Panama Canal Zone, Cuba and the Dominican Republic. The size of 150 mm of the specimen is the largest ever recorded for this species. The systematic position has been changed from Cephalaspidea – Philinidae to Anaspidea – Aplysiidae on the basis of unique shared conchological features of *Dolabella* and *Floribella*.

Key words: *Floribella*, Aplysiidae, Neogene, Caribbean.

INTRODUCTION

This paper is based on a single specimen from the early to early middle Miocene Baitoa Formation of the Northern Dominican Republic, which has been identified as *Floribella aldrichi* (Dall 1890), a rare species of seahare from the early Miocene of the Caribbean area. Due to the unusually large size and the rarity of the specimen the authors are of the opinion that it is worthwhile to publish a separate paper on this exceptional find.

The seahares are opisthobranchs in the order Anaspidea Fischer, 1993 [= Aplysiomorpha Eales, 1944: Although the rule of priority does not apply to taxa on the order level (ICZN-Code 1985, Mayr & Ashlock 1991: p. 395), the older name is used more and more], which are documented from the Jurassic to the present day (Skelton 1985). The earliest fossils of the genus *Dolabella/Floribella* (see below) are known from the early Miocene (Dall, 1890, see also Gardner 1937, Engel 1942, Wenz & Zilch 1959, Woodring 1970).

Today the herbivorous Aplysiidae occur from the intertidal zone down to 72 m in the open phytal, mostly throughout the world's tropical waters, but also in temperate regions (Eales 1921, Thompson 1976, Kandel 1979, Salvini-Plawen 1983). A few specimens have been recorded from deeper waters (Baba 1949, Kay 1979, Burn 1989), and occasionally in caves (Riedl 1966).

The largest aplysiid known, *Aplysia vaccaria* Winkler, 1955, attains a length of 990 mm and a wet weight of 14–16 kg (Burn 1989, Behrens 1991). The shell of this species, measures 316 ± 60 mm [$n = 2$: calculated from Eales (1960) and Kandel (1979)]. *Dolabella auricularia* (Lightfoot, 1786) is the largest representative of its genus and grows to up to 400 mm

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(Gosliner 1987), with its shell measuring 137 ± 16 mm ($n = 23$; calculated from Engel 1942, Eales 1944, 1979, Baba 1949, Abbott & Dance 1983, Springsteen & Leobrera 1986).

ABBREVIATIONS OF REPOSITORY INSTITUTIONS

The following abbreviations are used in this paper:

NBM: Naturhistorisches Museum Basel, Switzerland

USGS: United States Geological Survey

USNM: United States National Museum of Natural History, Washington, D.C., U.S.A.

SYSTEMATICS

Woodring (1970) placed *Floribella aldrichi* in the Philinidae within the order Cephalaspidea. The presence of a columellar callus, the presence of growth lines and the general outline of the shell are characters to *Floribella* and some Cephalaspidea and may have suggested this taxonomic placement to Woodring (1970). However, several characteristics of the shell of *Floribella* indicate a placement in the Anaspidea – Aplysiidae and not in the Cephalaspidea – Philinidae. The following characteristics in the apical region of the shell unite *Dolabella* and *Floribella* and separate *Floribella* from the Cephalaspidea: the thickening of the inner margin of the shell is continuous with a second shell layer, which covers only the apical region of the shell and bears spiral cords. This second layer abruptly terminates and leaves a scar-like mark on the growing edge of the dorsal layer (Figs. 2 and 3). These apical characters are only known from *Floribella* and *Dolabella*, strongly suggesting a close relation of the two genera. The outline of the shell perfectly fits an aplysiid form, growth lines can be easily observed in *Dolabella*, and a columellar callus is present in *Dolabella*, although the latter is greatly reduced to a narrow thickening on the outer margin of the shell. Therefore, we do not agree with Woodring (1970) and assign the genus *Floribella* to the Anaspidea – Aplysiidae. We restrict our discussion of the family to the three genera *Aplysia*, *Dolabella* and *Floribella*.

Genus *Floribella* Woodring, 1970

Type species (by original designation). – *Dolabella aldrichi* Dall. Early Miocene, Florida.

In contrast to *Aplysia*, the shell of *Floribella* is strongly calcified, spirally coiled and, in contrast to *Dolabella*, lacks a distinct knob-like apex. *Floribella* has more affinities to *Dolabella* than to *Aplysia*, but is to be placed in its own genus due to the much less reduced, and inflated shell.

Floribella aldrichi (Dall, 1890)

Figs. 1, 2, 4

Dolabella aldrichi Dall, 1890, p. 18 pl. 10, fig. 7a (early Miocene Chipola Formation, Florida); Gardner, 1937, p. 276, pl. 37, fig. 45 (Dall's illustration) (early Miocene Chipola Formation, Florida).

Floribella aldrichi (Dall), Woodring, 1970: 421, pl. 50, figs. 1.2, 5–8 (early Miocene La Boca Formation, Panama Canal Zone).

It is not possible to give a full description of this species on the basis of our specimen because it is too incompletely preserved. Reference is therefore made to Dall's original description (1890: reprinted by Gardner, 1937: 276) and to Woodring's (1970: 420–421) description of *Floribella* and his descriptive remarks on *F. aldrichi*.



Fig. 1. *Floribella aldrichi* (Dall, 1890). NMB 17439. Upper figure: Oblique "apical" view; lower figure: oblique "front" view of the same specimen. Scale bar = 2 cm.

Lectotype: USNM 328453. Selected by Woodring (1970:421).

Dimensions of lectotype: Height 18 mm, diameter 25 mm.

Type locality: USGS 2564, Chipola River on McClelland farm, 1 mile below bridge at old Bailey's Ferry, Calhoun County, Florida. Chipola Formation (early Miocene).

Material: Only one specimen (NMB H 17439) is available. It was collected on August 15, 1980 (Figs. 1, 2).

Measurements: Height 65 mm (incomplete), diameter 142 mm (incomplete), thickness of shell (where measurable) ranging from 1.1 mm to 3.6 mm (Fig. 4).



Fig. 2. Apical view of *Flonbella aldrichi* (Dall, 1890): NMB 17439: Note the secondary shell layer in the apical region and the spiral ridges. Scale bar = 1 cm.

Remarks: The unusually large specimen discussed herein was collected from a 3 m thick unit of greenish sands and silts with scattered fossils and two to three layers with molluscs. Although attached to the matrix the specimen is incompletely preserved. Its diameter is more than twice as large as the largest specimen figured by Woodring (1970, pl. 50, figs. 5, 7).

Fig. 3. Apical view *Dolabella auricularia* (Lightfoot, 1876): Collection Geiger OXE 02b: Japan, Wakayama. Note the secondary shell layer in the apical region and the spiral ridges. The maximum size of the shell is 39.6 mm.



Comparisons: So far *F. aldrichi* is the only species of its genus; therefore no comparative remarks can be given.

Occurrence: Specimen NMB H 17439 was found at NMB locality 17286: López section on Río Yaque del Norte, Dominican Republic, Baitoa Formation (late early to early middle Miocene). For geographic location and stratigraphic position of NMB locality 17286 see Saunders *et al.* (1986, pl. 9, figs. 1, 2; text-figs. 23–25, tables 1, 3, 4).

Distribution: Chipola Formation (early Miocene), Florida. La Boca Formation (early Miocene), Panama Canal Zone. Güines Limestone (early Miocene), Habana Province, Cuba (Woodring's 1970: 421 record). Baitoa Formation (late early to early middle Miocene), Dominican Republic.

RECONSTRUCTION OF THE SHELL

The size of the shell is one of the striking feature of the specimen at hand. We made a reconstruction of the whole shell from the specimen and pictures in the literature (Dall 1890, Woodring 1970). This resulted in a conservative estimate for the shell size of 150 mm (Fig. 4). As the outermost margin of the fossil shell is chipped, the complete shell of the living animal was a little larger.

SIZE OF THE ANIMAL

The size of the animal is assumed to have been larger than the shell, as in all members of the Anaspidea. The shell is already reduced to such an extent that the retraction of the whole animal into the shell seems highly unlikely. A reliable estimate of the animal size, however, proved to be difficult due to several factors. First, the shell of *Floribella* is much less reduced than in either *Dolabella* or *Aplysia*. It is difficult to assess the magnitude of this reduction in order to space the three genera on the x-axis in a regression analysis. Second, the estimate of the animal size has to be based on ratios of animal size to shell size for a variety of species in shells. Most authors gave measurements derived from preserved specimens and their shells. The process of preservation can alter the size of the animal greatly (Table 1), thus rendering an estimate of the animal impossible. These two problems introduce so much noise that attempts to determine the animal size of *F. aldrichii* had to be abandoned.

TABLE 1

Alteration of animal size due to preservation in some Aplysiidae. A/S-ratio: ratio of animal length to shell length. Factors of contraction due to preservation measured as live animal length divided by its preserved length. *: from preserved animal.

Species	A/S-ratio	Factor of contraction	Source
<i>Aplysia californica</i>	2.3	2.7	Marcus 1961
<i>Aplysia juliana</i>		1.4–1.6	Macnae 1955
<i>Aplysia maculata</i>	2.0*	1.5–2.0	Macnae 1955
<i>Aplysia parvula</i>			Clark 1984
		2.0	Macnae 1955
		2.7	Yonow & Hayward 1991
<i>Notarchus indicus</i>		3.0	Eales 1960
		3.45	Thompson 1977

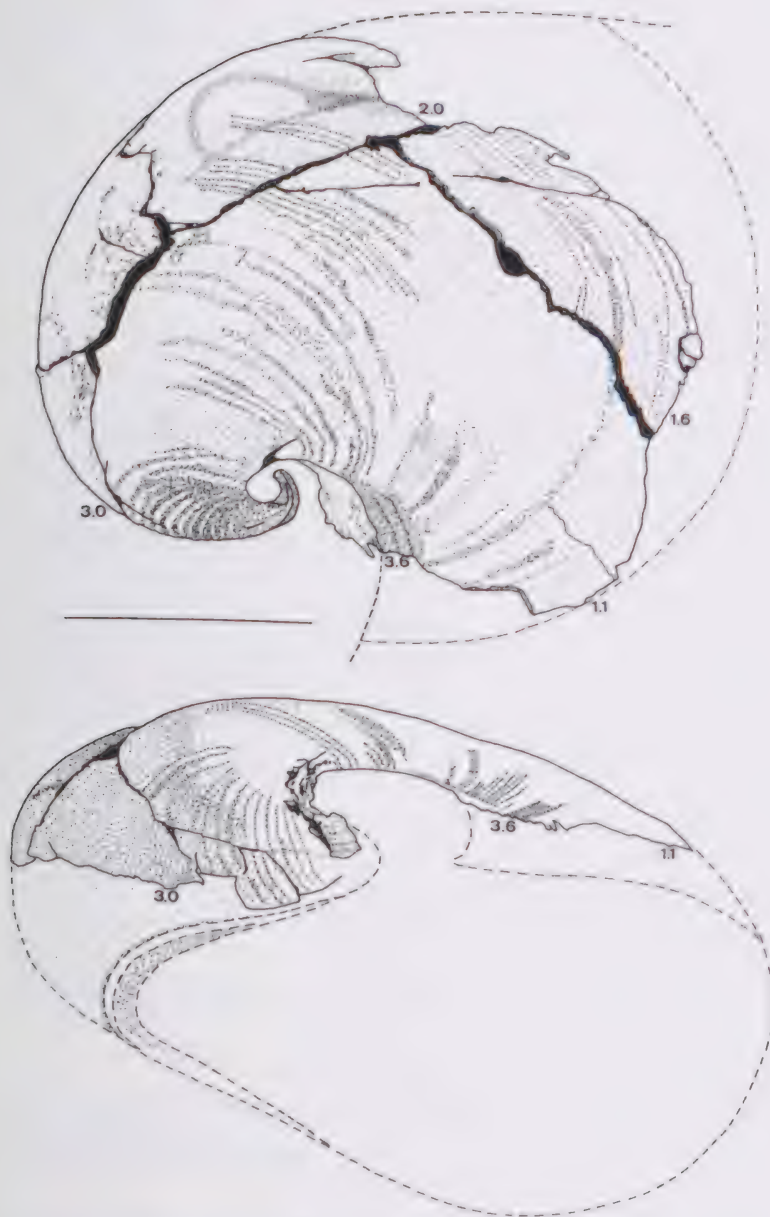


Fig. 4. Drawing of the specimen with indication of the thickness of the shell in mm. Scale bar = 5 cm.

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A NEW SPECIES OF THE GENUS *LEIOSTYLA* FROM THE MADEIRAN ARCHIPELAGO

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(Accepted for publication, 10th February, 1996)

Abstract: An undescribed *Leiostylia* collected on the 1995 field-recording expedition to Madeira by the National Museum of Wales is named as *Leiostylia colvillei* sp. nov. The shell is closely allied to the extinct species *Leiostylia wollastoni*.

Key words: Pupillidae, *Leiostylia*, Madeira.

INTRODUCTION

The genus *Leiostylia* is distributed through the Western Palaearctic with two principal centres of species diversity at opposite ends of this range on the Atlantic Islands (especially Madeira) and in the Caucasus. During the first century of malacological exploration in the Madeiran archipelago 28 species and subspecies of *Leiostylia* were described. The majority of Madeiran *Leiostylia* were found by Lowe (1831, 1852, 1854) and Wollaston (1878) during the period 1830 to 1870. Pilsbry (1923), whilst working on his monograph of the Family Pupillidae, described a further three species from the main island of Madeira. Recent fieldwork in the last twenty years has revealed an additional species from Madeira (Holyoak & Seddon, 1986) and a further three extinct species from Porto Santo (Seddon, 1990). Waldén (1983) provided a brief diagnosis of a new subspecies of *Leiostylia vineta*.

Over the last four years the National Museum of Wales has concentrated on sampling sites in deep ravines at intermediate and high elevations of the main island of Madeira. During the latest phase of fieldwork we obtained material of a *Leiostylia* species which differs from all those described.

SYSTEMATIC DESCRIPTION

Family Pupillidae

Genus *Leiostylia* Lowe, 1854

Leiostylia colvillei sp. nov.

(Plate 1a-d and Fig. 1a-b)

Type material: Three shells (2 fresh and 1 older) collected, in February 1995, by intensive sieving of leaf litter; all specimens deposited in the National Museum of Wales.

Holotype: NMW.Z 1995.004.001

Paratypes: NMW.Z 1995.004.002, NMW.Z 1995.004.003

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Measurements:

	Height (mm)	Breadth (mm)	Apertural height (mm)	Aperture as % of height
Holotype	2.65	1.5	0.9	33.9%
Paratypes				
(Fresh shell)	2.5	1.4	0.85	32%
(Dead shell)	2.8	1.5	0.9	34%

Type locality: Madeira. Valley of the Ribeira de Faja da Nogueira at 1000 m elevation, (c. 1.8 km west of the Power Station), in a small stream gully on the northern slopes of Pico Arreiro. Latitude 32°44'N, Longitude 16°56'W.

Description: The small cylindrical shell has 6 whorls with shallow sutures. It tapers slightly towards the mouth, as well as towards the apex, giving a shell form different from many species in the genus in that the widest point is not the body whorl. In a side view the upper edge of the mouth ascends slightly in the last 1/8 th of a whorl. The surface of the shell has regular, moderately developed, opisthoclinal ribbing giving a silky appearance. This is most conspicuous on the 4th and 5th whorl, absent on the first whorl and is reduced on the body-whorl, which in comparison is more glossy. The prominence of each individual rib is variable. Two of the type series are recent dead shells: these are both chestnut brown with no banding.

The aperture is auriform in shape and occupies 32–34% of the total shell height. The peristome is white, slightly reflected along the palatal margin. There are seven to eight whitish apertural teeth; an angular tooth, two columellar, one basal, two to three palatal teeth and one parietal tooth (terminology follows Pilsbry 1916, p. vii–ix). The angular tooth is the largest and most prominent feature of the aperture. It projects outwards from the mouth (Plate 1d), folding and curving in a spoon-shape obscuring the upper palatal tooth from front view (Plate 1b, 1c). The parietal is a simple, well developed lamella extending back into the aperture beyond view. The columella is thicker towards the upper portion, with a supracolumellar and a well developed columellar tooth inclined downwards towards the lower palatal teeth (Plate 1b). The smaller supracolumellar decreases in prominence towards the peristome, and has a simple form. The larger, columellar tooth has a flexuous form extending further back into the mouth merging into the columellar thickening before reaching the edge of the peristome (Plate 1c). The basal tooth is a simple rounded callus set back from the lip. The lower palatal is prominent although set back in the mouth; it is broad in shape, reaching upwards towards the parietal and columellar teeth and extending far back into the mouth. The interpalatal, when present, is a short lamella, arising from the same thickening as the lower palatal. The upper palatal is largely obscured from view, but is a well developed, sinuous fold extending to the edge of the lip, and descending into the mouth. There is a slight thickening along the lip between the upper palatal and the lip insertion on the body whorl with, on one shell, a small, slight, supra-palatal tooth.

Etymology: The specific name recognises Dr. Barry Colville who first found this species.

Habitat: The collecting site was on steep slopes and crags within *Erica arborea* L. and Laurel woodland. The specimens were extracted from litter samples collected from ledges on the north-west facing crags and slopes in a small stream gully, c. 150 m above the main river. The vegetation on the ledges comprised mainly grasses and ferns. The liverwort *Marchantia* covered extensive areas of vertical rock faces, particularly in the wetter areas. Above the small ledges and rock faces was an inaccessible terrace with a more diverse flora which included euphorbs and other herbs. In view of the very small area of habitat on the ledges it would seem possible that the specimens of *L. colvillei* had fallen from the terrace above.



Plate 1. *Leiostyla colvillei* n. sp. Holotype, NMW.Z. 1995.004.001. (a, top left) Full apertural view. (b, top right) enlarged frontal view of aperture. (c, bottom left) side view of aperture showing curved form of angular tooth. (d, bottom right) side view of aperture showing extension of the angular tooth.

The following molluscs were associated with *L. colvillei* in the litter samples taken from the small ledges, although not all were found alive: *Craspedopoma mucronatum*, *Leiostyla cheilogona*, *Columella microspora*, *Punctum pusillum*, *Phenacolimax* spp., *Spirorbula latens*, *Actinella*

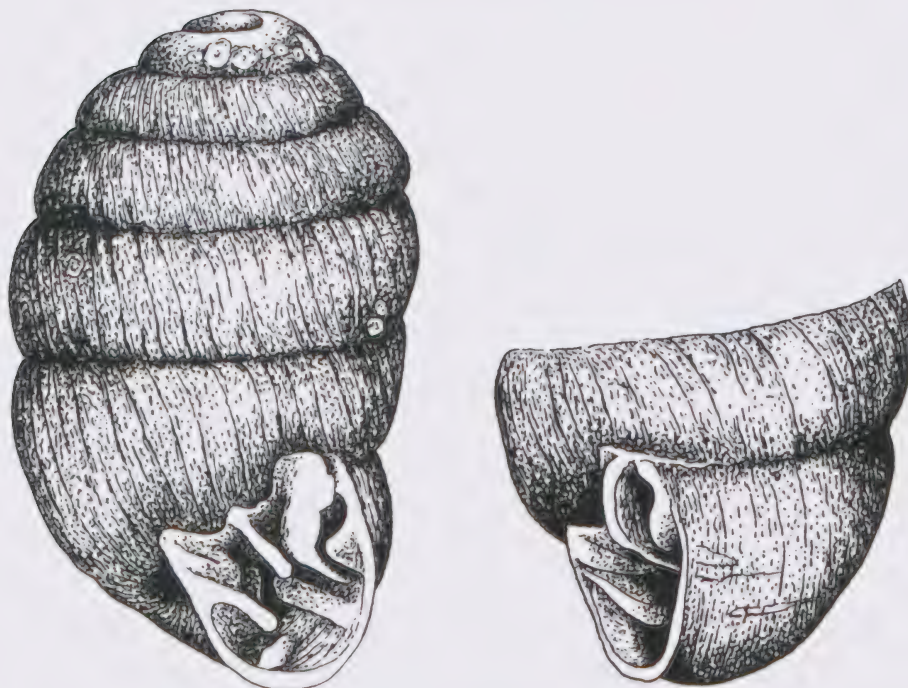


Fig. 1a & b. *Leiostylia colvillei* n. sp. NMW.Z. 1995.004.002 Paratype: whole apertural view and side view of aperture.

actinophora and *Leptaxis membranacea*. *Leiostylia loweana* was found frequently in *Marchantia* adjacent to the ledges.

Comparison: This is one of the smallest species of *Leiostylia*; the majority of the Madeiran species of *Leiostylia* are over 3 mm in length. The other small species include *Leiostylia millegrana* (Lowe, 1852), *Leiostylia wollastoni* (Paiva, 1866), *Leiostylia degenerata* (Wollaston, 1878), *Leiostylia gibba* (Lowe, 1852) and *Leiostylia abbreviata* (Lowe, 1852).

The most similar species is *Leiostylia wollastoni* which is known only as a fossil from the "piedade" deposits on the Ponta da São Lourenço. *Leiostylia wollastoni* has a similar size shell to *Leiostylia colvillei* but differs in having a slightly more cylindrical shape with the widest point at the body whorl. The most conspicuous differences are the entire shape and prominence of the angular and basal teeth. In *L. wollastoni* the angular is smaller and much straighter with a y-shaped link to the lip insertion and the basal tooth is stronger and well developed. The columellar tooth on *L. colvillei* is sinuous and drops into the mouth whereas on *L. wollastoni* it is thicker, less flexuous and projects towards the outer, rather than the lower lip. *L. wollastoni* has a more strongly developed parietal tooth. Some of the fossil shells show evidence of banding and a suprapalatal fold; these are not present in *L. colvillei*.

The other small *Leiostylia* species all show very strongly developed ribbing compared to the finer ribbing of *L. colvillei*. Like *Leiostylia gibba*, *L. colvillei* has a sinulus which is nearly closed but the angular, rather than the parietal and upper palatal fold, causes the construction. *Leiostylia gibba* is also characterised by the very broad shape, rather squat aperture and widely spaced ribbing.

Many of the *Leiostylia* species in the Madeiran archipelago occupy specialised habitats, with the more strongly ribbed species found in relatively dry sites. There are some ribbed

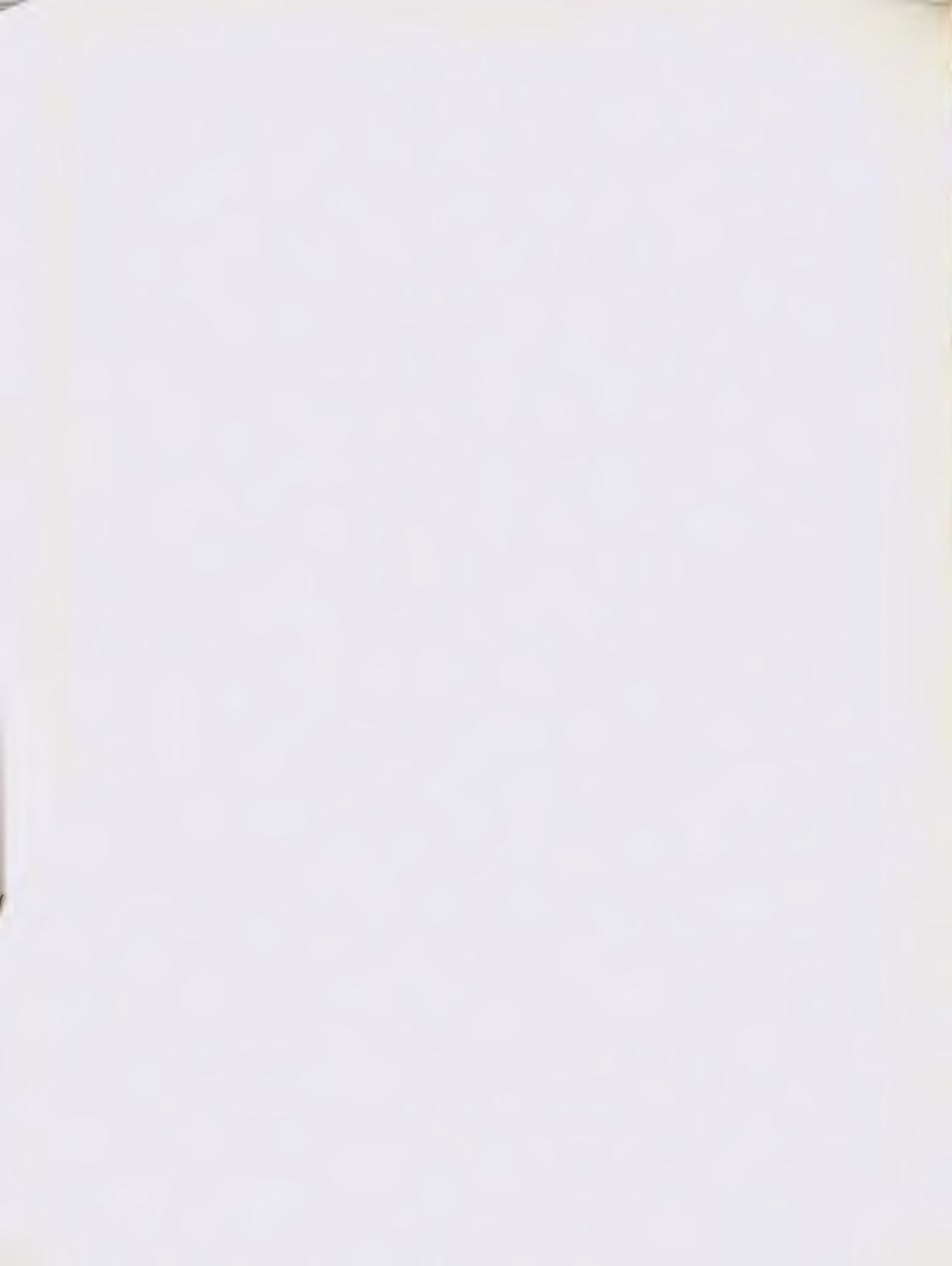
species with unknown habitats; *Leiostyla gibba* and *L. abbreviata* have not been found this century, and have only been collected once in a fresh state, in the valley of the Ribeira de Santa Luzia. Both are present as fossils along with *L. wollastoni*; the habitat of *Leiostyla wollastoni* is unknown as it has only been found in a fossil state. Cook *et al* (1993) found that *L. gibba* and *L. abbreviata* were present in the early Holocene deposits on the Ponta da São Lourenço, *L. gibba* was common in the late Holocene deposits (1600–200 years BP), but only single shells of *L. gibba* and *L. wollastoni* were found in the sediments deposited after human colonisation (approx. 1490 AD). Thus it is possible to infer that these species disappeared from the peninsula during the late Holocene, possibly after human colonisation. This may reflect a change in climate (drier) or a change in vegetation from woodland to grassland. The similarity between *L. colvillei* and *L. wollastoni* suggests that *L. wollastoni* was a woodland species. There are clear altitudinal ranges for some of the Madeiran species hence it is possible that *L. wollastoni* was the lowland species allied to *L. colvillei*.

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COMMUNICATIONS

ADDITIONAL RECORDS OF *HAWAIIA MINUSCULA* (BINNEY) AND *HELICODISCUS (HEBETODISCUS) SINGLEYANUS INERMIS* (BAKER) FROM SWEDEN

This communication provides additional records from Sweden of two species which have mainly been associated with synanthropic locations in northern Europe. To date only one record of *Hawaiiia minuscula* [von Proschwitz, T., *Fauna och flora* **78** (1983) pp. 277–284] and one of *H. inermis* [Waldén, H. W., *Fauna och flora* **79** (1984) pp. 29–43] have so far been published from these latitudes in NW Europe.

Hawaiiia minuscula (Binney, 1840) = 3 Swedish records: Prov. Västergötland, Göteborg, Botanical Garden, in the old orchid-house. Leg: T. v. Proschwitz 22–II–1982 [von Proschwitz, T., (1983) op. cit.]; Prov. Uppland, Uppsala, Botanical Garden, in the tropical hothouse. Leg: K. Martinsson 15–III–1994; Prov. Uppland, Stockholm, Bergianska Botanical Garden, in the *Victoria regia* house. Leg: T. v. Proschwitz 23–VI–1994.

This, native North American species, has with human help, been spread widely through the world. In Europe it was first recorded in the Botanical Garden in Belfast, Northern Ireland (Stelfox, A. W., *Proc. R. Ir. Acad.* **29B** (1911) pp. 65–165). Since then it has been found also in Scotland, England, the Netherlands, Germany and Austria [Kerney, M. P., Cameron, R. A. D. & Jungbluth, J. H. (1979) *Die Landschnecken Nord- und Mitteleuropas*. Paul Parey, Hamburg/Berlin]. In northern Europe it is a typical greenhouse inhabitant although it originally lives in areas with similar climate in Northern America. In Madeira and North Africa it is recorded in open-air habitats (Seddon & Holyoak, 1993 *J. Conch., Lond.* **34**: 321–332). The new Swedish records are all made in hothouses of major botanical gardens conforming to the normal situation in Europe. In Stockholm numerous living specimens were found in the *Victoria regia*-house in the side-beds containing tropical plants. In Göteborg a living specimen and an empty shell were recorded under flower-pots in the old orchid-house and in Uppsala a single empty shell was found in a soil sample from the tropical hothouse, containing *Lamellaxis clavulinus* (Potiez & Michaud) [cf. von Proschwitz, T., *J. Conch., Lond.* **35** (1994) pp. 184–185]. The main means of dispersal for *H. minuscula* is probably passive dispersal with plants and soil as shown also by its occasional occurrence in flower-pots. In Bavaria, Germany it has been found several times in pots with *Yucca-palms* (*G. Falkner, München, pers. comm.*).

Helicodiscus singleyanus inermis (Baker, 1929) = 3 Swedish records: Prov. Skåne, Lund, Botanical Garden, in the hothouses. Leg: U. Gårdenfors 18–XI–1981; Prov. Halland, Laholm, Lagaholm, in archaeological excavation of medieval grave-field. Leg: A. Andersson 1980 [Waldén, H. W., (1984) op. cit.]; Prov. Uppland, Stockholm, Bergianska Botanical Garden, in the old abandoned glasshouse. Leg: T. v. Proschwitz 23–VI–1994.

The first European record of *Helicodiscus singleyanus inermis* was from the Netherlands in 1943 [Kuiper, J. G. J., *Arch. Moll.* **85** (1956) pp. 163–169]. Later records have been made in several countries: England, the Netherlands, Belgium, France, Spain, Switzerland, Germany, Austria, Hungary, Czechoslovakia and Poland [van Regteren Altena, C. O., *Basteria* **25** (1961) pp. 41–43; Chatfield, J., *J. Conch., Lond.* **29** (1977) pp. 137–140; Kerney, M. P., Cameron, R. A. D. & Jungbluth, J. H. (1979) op. cit.]. It should be noted that at least two species of the subgenus *Hebetodiscus* occur in Europe. The name '*inermis*' is here used for the small form lacking distinct spiral stria, which has been recorded in the Netherlands, Madeira (Walden, 1983, *Ann. Zool. Fennica*, 636) and N. Africa (Seddon & Holyoak, op. cit.). I consider that *inermis* is a separate species, distinct from *H. singleyanus* (Pilsbry), although it is usually regarded as a subspecies. The identity of the *Hebetodiscus*-species found in Europe and their affinities to the North American forms, are, however, far from clear.

The presence of this species in Europe has been attributed to introductions by man, but the records from archaeological contexts might suggest that it is an overlooked indigenous species. In Sweden it is, however, most certainly introduced. The two greenhouse records indicate introduction with plants as the means of dispersal. The origin of the specimens, found during the archaeological excavation at Laholm seems more uncertain, but possibly the species has also been introduced with ornamental plants. The subterranean habit is in good accordance with records from other parts of Europe. One of the first records of the species in Great Britain (La Bergerie, Jersey) was also from an archaeological excavation [Chatfield, J., *J. Conch., Lond.* **29** (1977) pp. 137–140]. None of the Swedish specimens were alive when found and none of the shells contained the remains of the animal. The shells from Laholm and Lund, however, give a fresh impression and the specimens seem to be recently dead, whereas the one from Stockholm seems to be have been dead for some time.

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REDISCOVERY OF "EXTINCT" LAND-SNAILS ON MADEIRA

The land molluscs of the Madeiran archipelago are well known for their endemic radiation and have consequently received much attention from conservationists. The original Red Data book for invertebrates (IUCN 1983, Cambridge) indicated that there were 16 species which had not been recorded since the nineteenth century and suggested that these may have become extinct. Since then this data has been repeated in subsequent Red Data Books and in "Global Biodiversity" (Groombridge, 1992 Chapman & Hall, London). Several of these extinct species are from the genus *Leiostryla* which is well-known for its separate radiations on each island of the archipelago, with some 30 taxa now recorded (Waldén 1983, *Annales Zoologica Fennica*, **20**: 265–275; Pokryesko & Waldén 1992, *Proc. 10th intern. Malacol. Congr. Tübingen* pp. 565–570). In his book, *Testacea Atlantica*, Wollaston (1878 London, Reeve) gave detailed comments on the distribution and ecology of the family Pupillidae, and this still provides the most comprehensive data available on the status of the rare species. Recent survey work on the main island of Madeira has led to descriptions of new species of *Leiostryla* (Waldén 1983 *op. cit.*, Holyoak & Seddon 1986, *J. Conch. Lond.*, **37**: 191–193; Seddon & Killeen, 1995, this volume).

The National Museum of Wales has been surveying some of the remote valleys in the centre of the island, as part of a research programme on the Molluscan Fauna of the Madeiran Islands. During the 1993 phase of fieldwork, we obtained material of two species of *Leiostryla* which have not been recorded in the literature since (the 1870s). Several populations of *Leiostryla laevigata* (Lowe, 1852) and *Leiostryla concinna* (Lowe, 1864) were found in remote parts of the Parque Regionale de Madeira between elevations of 1200 and 1700 m. The details of the localities are not given to protect these species. Several of the sites were small ($>50\text{ m}^2$) and thus each species remains extremely vulnerable to habitat disturbance, and potentially extinction. As the result of this work their status was amended to vulnerable in the latest copy of the IUCN Red list (Groombridge, 1994; IUCN, Cambridge).

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BOOK REVIEWS

Atlante delle Conchiglie Marine del Mediterraneo (Atlas of the Mediterranean sea shells) Volume 1 (Archaeogastropoda) by R. Giannuzzi-Savelli, F. Pusateri, A. Palmeri and C. Ebreo. Edizioni de "La Conchiglia", Roma, Italy. ISBN 88-86463-00-6, 1994. 125 pp, 395 (mostly colour) plates. 80,000 It. Lire.

This book is another in the line of high quality colour photographic guides on molluscs currently being published in Italy. One could only wish that such works were being funded for the British fauna; marine bivalves or freshwater gastropods for example.

It is the intention of this work to be the first volume in a set that would illustrate all of the species in the *Annotated checklist of Mediterranean marine mollusks* (Sabelli, Gianuzzi-Savelli & Bedulli 1990). Even the writer of the Foreword admits that this is an extremely ambitious and even slightly mad programme. There is no doubt that when completed this will be a valuable reference work.

This hardback, A4 book comprises a Foreword and a 2 page introduction in both Italian and English text. The Introduction gives background to the different Orders of archaeogastropods. There are several references to other works given in this section but they do not appear in full elsewhere in the book. This is followed by a systematic list of 146 species and sub-species, which follows Sabelli *et al* (1990) apart from minor nomenclature and taxonomic changes.

The remaining 100 pages of the book are made up of colour plates with all 146 species illustrated. The authors have included different colour morphs of many species, which amounts to 664 photographs. *Calliostoma laugieri* and *Jujubinus exasperatus* for example each have a complete page of plates. Mostly the quality of the colour plates is very good although in some cases sculptural detail is lost because of the soft image.

Most of the small, deeper water limpets and the scissurellids are illustrated by good quality SEM photographs. The "skeneomorphs" are also illustrated by SEMs, although most (or all) are taken from Waren's 1992 work (*Boll. malac.* 27: 149-247). Some of the commoner species are also illustrated by a colour photograph. This is unnecessary because the majority are slightly fuzzy and the quality of the specimens is not good, the specimen of *Dikoleps nitens*, for example, is worn and has a sand grain in the aperture! This is the same problem as in the *The Atlas of shells from the central Adriatic Sea* (see Review *J. Conch. Lond.* 34: 397). These shortcomings should be picked up at the editorial stage.

The front cover of this book is misleading. Unless you were to look at the title page or the small print on the spine you might be under the impression that this book covered more than just archaeogastropods. It was not until flicking through the plates and thinking that *Tricolia* was a strange species to have on the last page that I realised that this was not the case. I suspect that the sub-title (Vol. 1-Archaeogastropoda) may well be omitted from some catalogues and buyers will get less than they bargained for.

Despite these minor grumbles it is still a beautiful book. It is clearly aimed at a wide market, the colour work combined with the inclusion of all species means that it will be of use to both the amateur shell collector and taxonomists and the cost of around £90 is not unreasonable. However, by the time all mollusc groups are eventually covered (>6 volumes) it will be quite an expensive work. One can only hope that the enormity of the task and increasing publishing costs will not prevent the work from being completed.

IAN KILLEEN

BIOMÖR I: Benthic Biodiversity in the Southern Irish Sea. Andrew S. Mackie, P. Graham Oliver & E. Ivor S. Rees. May 1995. National Museum of Wales. ISBN 0 7200 0427 6 £30.00 softback.

As Marine Recorder I am always interested to hear that major marine benthic surveys are carried out by commercial companies or other organisations as these are a potentially valuable source of biogeographical data for the Society's Census schemes. However I am also frequently frustrated by the fact that the results are never published or that release of data is 'difficult' for commercial reasons. It is, therefore, a delight to see the results of a comprehensive survey published in full.

The publication of this first Biomör report marks the completion of a significant phase of research in the marine areas around Wales. Two surveys of benthic invertebrates in the southern Irish Sea were carried out in 1989 and 1991 during which some 1030 species were recorded. The area is important as it has a fauna reflecting its position as a boundary between 2 biogeographical provinces (the Boreal province of the north and the Lusitanian to the south) and yet large parts of the Irish Sea were and still are poorly known. The sampling programme consisted of dredged and grabbed stations to obtain biological material for taxonomic investigation, determination of faunal composition and diversity of assemblages, and eventual integration into the Museum's reference collections. An important feature of this survey was that the samples were sieved over a 0.5 mm mesh sieve rather than the conventionally used 1 mm or 2 mm mesh. In addition, sediments were collected for analysis and seabed photography enabled still visual images to be obtained.

The integration of all this primary data has enabled the production of a substantial, comprehensive and highly

informative report. Chapters on Historical Perspective, Sampling Methods and Treatments, and The Study Area precede the body of the report which describes the Benthic Macrofauna. Annelids dominate the fauna which is 80% infaunal and 20% epifaunal. The second and third largest groups were Crustacea and Mollusca. Each of these major groups is discussed in a separate section and new problems with taxonomy are addressed. This has resulted in the recognition of synonymies as well as descriptions of new species. Altogether, seven sections within the Macrofaunal chapter have been contributed by experts.

One of the great strengths of this report is the inclusion of a chapter dealing with Classification and Ordination. In this chapter the statistical methods used to define communities and assemblages are outlined, discussed and compared. The chapter is extensively illustrated with graphs and tables to depict the techniques and individual tests used and show the results. For completeness, all the raw data are included in the report as a set of Appendices enabling the reader to analyse the results for himself.

Final chapters describe the macrofaunal assemblages recognised by integrated analysis of the data and also identify species diversity using diversity indices. An Overview summarises the findings within 3 concise pages. An extensive bibliography and over 100 pages of appendices appear at the end of the report.

Members of this Society will be interested in the molluscan data which is discussed in a section contributed by Ian Killeen. Over 150 species were found alive (77 bivalve and 61 gastropod species). Amongst these data are many new, and updated from shell only, Sea Area records, particularly for S21 and S22. Many of these are for the smaller species such as *Dikoleps nitens* and *Caecum glabrum*, elements that are frequently missed by sieving over too coarse a sieve. So-called northern species such as *Emarginula crassa* or *Pulsellum lafosense* were found living in deep water whereas previously recorded southern species such as *Galeodea rugosa* and *Callista chione* were not found. It is especially pleasing to see that the Caudoloveates and Solenogastres were collected and identified. Eight species were found, considerably increasing our knowledge of their distribution and ecology in British waters. Four of the mollusc species are illustrated including a very useful drawing of a juvenile *Lutraria lutraria*.

The report is published as a high quality A4 paperback and contains numerous figures and tables. The faunal distribution and facies maps are clear with the clever use of a limited range of grey and blue shades. Perhaps the use of more colours would have rendered the distributions more distinctive although this would have increased the production costs significantly. As it is, the sponsorship of the Marathon Oil Company has enabled a thorough record and elegant presentation of the research cruises and their results.

To call this publication a 'report' is to undersell its potential use and application. It sets a new benchmark for its genre. The comprehensive coverage of all aspects of the 2 surveys – it stops short of outlining the menus that were available to the crew and scientists aboard! – means that it is a useful text for students and workers in marine sciences and for benthic ecologists and serves as a model for others contemplating similar surveys.

JANICE M. LIGHT

INSTRUCTIONS TO AUTHORS

Manuscripts should be sent to:— **The Hon. Editor, Dr P. G. Oliver, National Museums & Galleries of Wales, Cathays Park, Cardiff CF1 3NP.**

PAPERS Two copies of text and illustrations should be submitted; one set of illustrations must be good quality originals. Authors should refer to recent copies of the *Journal* for a guide to format. Authors are reminded of the high cost of printing and therefore are expected to write concisely and to make maximum use of page size when designing art-work and tables.

COMMUNICATIONS These are intended to be short notes of an original nature which do not merit the treatment of a full paper. *Communications* must not contain any figures, tables or plates and should conform in style to that of recent issues of the *Journal*.

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